Spoilage of Haddock in the Trawlers at Sea: The Measurement of Spoilage and Standards of Quality[1, 2]

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ABSTRACT

During a period of eight months, 850 haddock were taken from a trawler from the Nova Scotian and Grand Banks. Immediately after landing, the fish were filleted and the fillets were examined organoleptically and tested for pH and trimethylamine.

The results indicate a rather close correlation between the development of early spoilage odours and the increase of trimethylamine. One marked exception was the development of "bilgy" odours which can become very offensive without an increase in the trimethylamine content of the muscle.

Sixty-five per cent of the fillets without perceptible spoilage odours had trimethylamine values[3] of less than 1 mg. per 100 g.; 83 per cent had values of less than 1.5 mg., 92.5 per cent of less than 2 mg.; only 0.5 per cent had trimethylamine values of between 3 and 4 mg. and none above that level. Conversely, only 10.5 per cent of the "smelly" fish had trimethylamine values below 1 mg.; 89.5 per cent had values above 1.0 mg., and 66.5 per cent above the 1.5-mg. level. For the purpose of grading freshly cut haddock fillets, the following standards are suggested: trimethylamine values of 0 to 1 mg. per 100 g.–fresh; 1 to 5 mg.–doubtful or spoiling; above 5 mg.–spoiled.

In spite of its usefulness as a measure of spoilage, it seems very unlikely that trimethylamine contributes to the early spoilage odours that develop in haddock muscle before the pH reaches 6.9.

The pH of the homogenized muscle is not a good indication of the extent of deterioration that takes place in the earlier stages of spoilage of these fish.

INTRODUCTION

The present paper is the first in a series of studies dealing with spoilage of haddock in trawlers at sea. The ultimate aim of this work is to improve the quality of the fish at the time of discharge at the wharf. To do this, both why and where fish undergo deterioration in handling and during stowage aboard the vessels must be learned. And, more particularly, the relative importance of the factors that contribute to their deterioration should be known.

Immediately the problem arises of finding a suitable method for measuring the amount of spoilage that takes place in the gutted or round fish in the vessels.

It would be an immense task to use simultaneously, and to attempt the evaluation of, all the methods that are now available for measuring spoilage. But enough work has been done to indicate that for some species of fish certain tests are more valuable than others. The amount of trimethylamine, for example, has

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[3]In this series of papers, "trimethylamine value" indicates mg. of trimethylamine nitrogen per 100 g. of fish.

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been shown to be one of the most useful criteria for spoilage in Atlantic cod and haddock (Beatty and Gibbons, 1937), as well as for certain other species of sea fish (Sigurdsson, 1947; Hol'mov, 1939; Shewan, 1949). However, much of the data indicating its usefulness has been based on tests using muscle press juice and minced or whole fillets. Whether it is equally useful as a measure of spoilage for gutted fish held under the different environmental conditions that might be encountered in vessels at sea is another question. Furthermore, even if the value of trimethylamine were proven, it would not be certain that the levels of trimethylamine associated with the various degrees of spoilage in stored fillets are equally applicable to the muscle of unfilleted fish. We are also confronted with the problem that definitely spoiled cod and haddock have occasionally been observed with very low trimethylamine values.

Therefore, in this first portion of these studies, the value of trimethylamine as a measure of spoilage has been re-examined and compared with organoleptic ratings, with particular reference to gutted haddock at the time of their discharge from Canadian Atlantic trawlers.

EXPERIMENTAL METHODS

The principal data deal with haddock caught during 20 trips to the Nova Scotian and Grand Banks during the months from February to September inclusive, 1953. These fish were all caught by the same fishing vessel, iced down in the normal manner by the regular crew, and were filleted under commercial conditions immediately after the boat was discharged. They included fish that had been iced down in the hold for from one to nine days at the time of landing.

No attempt was made to examine or grade the whole gutted fish. All tests and all examinations were made on the fillets, which were freshly cut from the fish immediately after they were discharged from the boat.

The organoleptic procedures were purposely made as simple as possible. Each fillet was examined for odour, colour and texture, and recorded as either "fresh" or "not fresh". Almost every fillet that was recorded as "not fresh" was one that had developed perceptible spoilage odours. Occasionally, however, fish were marked "not fresh" when the fillet was discoloured or soft but without a noticeable off-odour. These gradings were made independently by at least two persons who knew nothing of the history of the fish.

If the fillet was small, that is under 150 g., the whole fillet was ground in a Waring blendor with twice its weight of distilled water. With large fillets three strips of approximately 50 g. each, cut crosswise through the nape, centre and tail sections, were used. The pH and trimethylamine determinations were made from this homogenate. The pH readings were obtained with a glass electrode, using a Beckman pH meter. Trimethylamine was measured colorimetrically, using the method described by Dyer (1945, 1950).

As can be seen from the tables, most of the fish that were examined had been iced in the hold of the vessel for from four to seven days. This was done purposely because it was during this period that many of the fish began to show definite signs of deterioration.

Amount of Trimethylamine and the Freshness of Fish

If trimethylamine is used as a measure of freshness, at what point may we assume that there is a significant loss in the initial quality of the fish? Beatty and Gibbons (1936), working chiefly with cod muscle press juice, were of the opinion that odours first begin to appear when the trimethylamine value is about 4–6 mg. per 100 ml. of press juice and that very definite odours are present at 10 mg. Notevarp (1943) is of the same opinion: the trimethylamine content of "fresh fish" is between 0.6 and 5 mg. per 100 g. and that of fish that is "doubtfully fresh" is 10 mg. Shewan (1949) also comes to the same conclusion: when the trimethylamine value reaches 4–6 mg. per 100 ml. of press juice, the fish spoilage odours are developing. Hol'mov (1939) reduces the figure still lower, observing that "fresh fish" have a trimethylamine value of less than 1 mg. and that initial spoilage is taking place when the value reaches 3 to 5 mg. In taste panel studies, Dyer and Dyer (1948) pointed out that the palatability of fish is lowered before actual spoilage odours become evident; than an increase from 0 to 1 mg. of trimethylamine nitrogen was accompanied by a change from a "fresh sea tang" to a more or less tasteless product, and that further increases were accompanied by some of the early spoilage flavours and odours and a decrease in the grading score of the fish.

Many other observations could be quoted showing that initial spoilage odours are present when the trimethylamine value reaches a point somewhere below 4 or 5 mg. per 100 g. If the rate of trimethylamine production showed a constant increase with time, we might be forced arbitrarily to select a point between 0 and 5 mg. per 100 g. of fish, as a borderline between strictly fresh fish and fish of doubtful quality. But the rate of trimethylamine formation is not constant. Many studies have demonstrated that (as in Figure 1) after a first slow initial increase, trimethylamine formation becomes much more rapid. In haddock muscle examined in this work the change in the slope of the trimethylamine curve became evident when the values reached approximately 1–1.5 mg. per 100 g. This would seem to confirm the observations of Hol'mov and Dyer, as mentioned above, that fish are no longer strictly fresh once the trimethylamine value has reached approximately 1 mg., and that, if they do not already show signs of spoilage, they will do so shortly.

Therefore, for use in this paper, a trimethylamine value under 1 has been arbitrarily chosen as indicating fresh fish; 1 to 5 mg. as fish that are doubtful or spoiling; and over 5 mg. as spoiled.

There is much less foundation for picking a pH value that will separate "fresh" from "doubtfully fresh" fish. However, for the purpose of having something definite to start with, we have assumed here that haddock muscle with a pH of 6.7 and over is no longer strictly fresh.

EXPERIMENTAL RESULTS

A General Picture of the Condition of the Fish

During a period of eight months the fillets from 850 haddock were examined and tested. There were usually from four to six fish in each lot that were tested together.

Figure 1 shows the mean values for trimethylamine and pH for these fish in relation to the number of days they had been stored in ice on the boat. This is a typical trimethylamine curve for muscle of fish of the cod family. For approximately six days there is a slow, consistent increase in the values until a point somewhere between 1 and 2 mg. is reached; after this the rate of trimethylamine formation is accelerated.

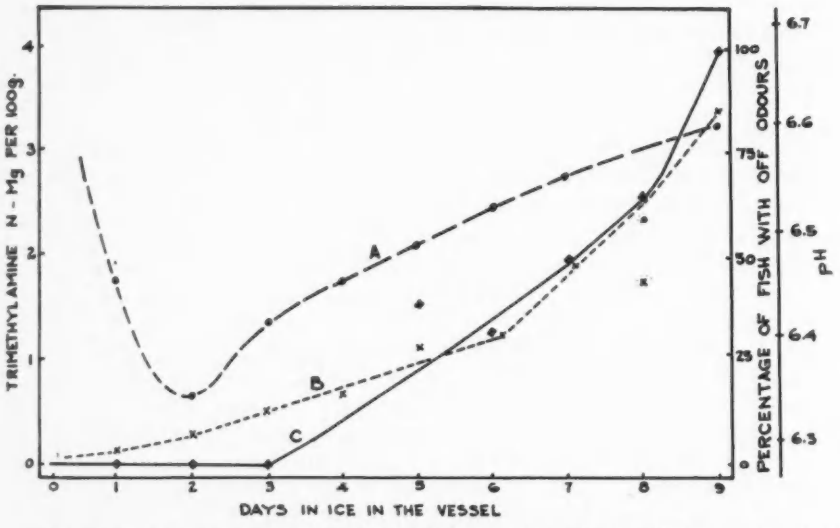

FIGURE 1. The mean pH (A) and trimethylamine (B) values, and the percentage of fillets graded "not fresh" by organoleptic examination (C) of 850 freshly cut haddock fillets from fish that had been held in ice in the hold of the vessel for from 1 to 9 days.

The pH curve roughly approximates that of the trimethylamine. After the initial drop accompanying the changes in the muscle up to the end of rigor mortis, there is a gradual increase from a low mean of pH 6.3 at two days to 6.6 at nine days.

Table I shows trimethylamine values in greater detail. It shows as well that the mean values are statistically significant. When these fillets were classified according to our arbitrary standards of spoilage based on trimethylamine values, the results shown in Table II were obtained. Up to four days in ice, all the fish gave first-grade fillets. Between four and six days there was a sharp reduction in first-grade fish and a corresponding increase in spoiling or doubtful fish. With further storage this trend continued until nine days, at which time almost one-fifth of the fish were spoiled and few, if any, of the remainder were strictly fresh.

The results from organoleptic examination of these fillets gave very much the same picture: up to three days all the fillets were judged fresh; 11 per cent were beginning to spoil at four days; and from then until nine days the percentage of spoiled fish continued to increase daily; at nine days none of the fish was judged to be fresh.

This rather general picture simply confirms what we already know: that spoilage increases with time and that, as the fish spoil, there is a tendency for the pH to increase and the trimethylamine to accumulate.

TABLE I. Trimethylamine values from 850 haddock fillets freshly cut from fish that had been iced in the vessel for from 1 to 9 days at sea.

Days in ice	No. of fillets tested	Mean trimethyl-amine value	Standard deviation of means	Standard deviation of individuals	Maximum trimethyl-amine value	Minimum trimethyl-amine value
1	12	0.18	0.072	0.021	0.28	0.07
2	12	0.29	0.033	0.11	0.49	0.16
3	14	0.57	...	...	0.84	0.34
4	149	0.67	0.031	0.37	1.8	0.12
5	118	1.15	0.057	0.62	2.6	0.10
6	208	1.22	0.053	0.58	3.1	0.10
7	223	1.82	0.062	0.89	4.0	0.10
8	70	1.80	0.13	1.14	5.9	0.30
9	44	3.35	0.21	1.36	6.0	0.50

TABLE II. The percentage of fillets in increasing ranges of trimethylamine, from 850 haddock iced in the vessel for from 1 to 9 days at sea.

Days in ice	Percentage of fillets with trimethylamine values of					
	0–0.9	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	over 5
1	100	0	0	0	0	0
2	100	0	0	0	0	0
3	100	0	0	0	0	0
4	82	18	0	0	0	0
5	46	41	13	0	0	0
6	44	38	15	3	0	0
7	17	42	26	13.5	1.5	0
8	20	44.3	20	10	4.3	1.4
9	2	16	25	25	14	18
	fresh	spoiling				spoiled

(arbitrary standards of spoilage based on trimethylamine values)

COMPARISON OF THE RATINGS OBTAINED BY USING ODOUR, pH AND TRIMETHYLAMINE AS CRITERIA OF SPOILAGE

Every fillet was graded "fresh" or "not fresh" using each of the arbitrarily selected standards based on odour, pH and trimethylamine. The results are given in the first three columns of Table III. It can be seen that the percentage of fish graded "fresh" is always greatest using the pH criterion, and least with the trimethylamine. Even after nine days in the hold, almost 80 per cent of the fish were judged "fresh" where pH alone was the measure of freshness; at this period the same fish were all rated "not fresh" by their odour or their trimethylamine values.

TABLE III. Percentages of fillets judged to be "fresh" by using trimethylamine (under 1.0 mg./100 g.), pH (under 6.7) and odour as measures of freshness; and the reduction in the percentage of "fresh" fish when the results from pH and odour are combined with those from trimethylamine.

Days in ice	Percentage of fish judged "fresh" by			Further reduction in the percentage of fish judged to be "fresh" when pH and odour are used as additional criteria of freshness		
	pH	Odour	Trimethylamine	Trimethylamine +pH	Trimethylamine +odour	Trimethylamine +pH+odour
1	100	100	100	0	0	0
2	100	100	100	0	0	0
3	100	100	100	0	0	0
4	99	89	82	1	7	8
5	94	66	46	1	4	4
6	83	71	44	3	5	8
7	81	54	17	4	1	5
8	86	34	20	3	4	7
9	77	0	2	2	2	2

It appears obvious, then, that trimethylamine is a more sensitive measure of the early changes taking place as the muscle spoils than either odour or pH. The question arises, what proportion of the fish that are rated "not fresh" by the odour or pH criterion are rated "fresh" by the trimethylamine content? The answer can be seen in the last three columns of Table III. The use of pH in addition to trimethylamine reduced the percentage of "fresh" fillets by 1 to 4 per cent; the use of odour reduced it 1 to 7 per cent. The addition of both odour and pH reduced it by 4 to 8 per cent. It can be seen from these figures that very few of the fillets rated "fresh" by the trimethylamine content were judged to be "not fresh" by both odour and pH.

These figures in Table III refer to the percentages of all the fish that were graded by using these three criteria. However, if they are recalculated in terms of 100 per cent for those indicated as "not fresh" by the trimethylamine, we get the

TABLE IV. Increase in the percentage of samples rated as "not fresh" when odour and pH (6.7 and above) are used as additional measures of spoilage and calculated in terms of 100 per cent for those judged "not fresh" by their trimethylamine (1.0 mg. and over per 100 g.) content.

Days in boat	Additional criteria of spoilage		
	pH	Odour	pH+odour
4	1.2	8.5	9.7
5	2.2	8.9	11.1
6	6.8	11.4	18.2
7	23.6	5.9	29.4
8	15.0	20.0	35.0

figures shown in Table IV. This indicates a trend showing that, as the fish get older, the addition of pH measurements may be of some value; and that on the average the use of odour as a measure of spoilage may add a little to the numbers of fish judged "not fresh" by trimethylamine alone. It can also be seen that, for the fish stored in the boat from four to nine days, the combined use of odour and pH added about one-fifth to the number of fillets graded "not fresh" by trimethylamine alone.

Trimethylamine Levels of "Smelly" and "Non-Smelly" Fish

Of the 850 fish that were examined, 308 were rated "not fresh" and 542 were rated "fresh" by organoleptic examination of the freshly cut fillets. Actually this simply divided the fish into two groups: those which showed no perceptible change, and a second group containing fish that varied all the way from those having a very faint spoilage odour to those that had developed very pronounced spoilage odours. The percentage of fish in the different trimethylamine levels was calculated separately for the "smelly" and the "non-smelly" groups and is shown in Table V.

Table V. Percentage of the 308 "smelly" and 542 "non-smelly" fish in various trimethylamine levels.

Trimethylamine level	"Smelly" fish	"Non-smelly" fish
mg./100 g.	%	%
0–1	10.5	65
1–1.5	23.0	18
1.5–2	17.5	9.5
2–3	28.2	7.0
3–4	14.3	0.5
4–5	3.5	0
over 5	3.0	0

Fish that were free from spoilage odours did not invariably have trimethylamine values below the 1-mg. level that was arbitrarily chosen as the limit for "fresh" fish. And conversely, some of the fish that were definitely spoiling had values below this 1-mg. level. However, there does appear to be a very definite relationship between the appearance of these early spoilage odours and the development of trimethylamine. Sixty-five per cent of the "non-smelly" fish had values below 1 mg., 83 per cent below 1.5 mg., and 92.5 per cent below 2 mg.; the values of only 0.5 per cent were between 3 and 4 mg., and none were above that level. And conversely, only 10.5 per cent of the "smelly" fish had values below 1 mg., 23.5 per cent below 1.5 mg., while the values of 65.5 per cent were above the 1.5-mg. level.

Particular Types of Spoilage

The results up to this point have been obtained by examining the data indiscriminately from all the fish that were tested. They do show very definite

trends, such as those indicating the rather close relationship between trimethylamine value and the development of early spoilage odours, and the general tendency for the pH of the fish to rise as the odours become offensive. However, when we examine what appear to be specific types of spoilage, we find that the relationships shown in these trends are not always valid.

BILGY FISH

During the winter and early spring, fish from six to eight days on ice, and more particularly those at the bottom of the pens or those pressed tightly against the pen boards or shelves, develop a very offensive odour suggestive of pig manure or bilge water and described by fishermen as "bilgy" fish. Such fish usually have a comparatively low pH and there is no apparent relationship between the trimethylamine value and the presence or intensity of the odour. A typical example of this can be seen in the data given in Table VI. In this particular instance a whole pen was iced down with haddock caught on the same day. When the vessel was docked, five fish were taken from each of the ten different locations indicated in this table. The figures given are the average values for each lot of five fish. Neither the pH nor the trimethylamine gave any indication of the condition of the fish. This particular type of spoilage is characterized by the following: it develops under an anaerobic environment; it is associated with heavy contamination from fish faeces; the spoilage products are acidic and the vile odours are almost completely neutralized with alkali.

TABLE VI. Odour, trimethylamine and pH values of 50 haddock fillets cut from fish that had been stored 6 days in ice in 10 different locations in the pen. Each figure is the average value obtained from 5 fish. (Each pen is divided into three levels by inserting two sets of shelf boards.)

Location in pen	Odour	Trimethylamine	pH
		mg./100 g.	
1. Top level—against back wall	Fresh	0.79	6.40
2. Second level—centre top	Fresh?	1.56	6.50
3. Second level—centre	Fresh?	1.20	6.50
4. Second level—centre front	Fresh	0.90	6.45
5. Second level—against back walls	Stale	1.44	6.45
6. Bottom level—centre top	Fresh	0.69	6.40
7. Bottom level—centre	Fresh to slightly faecal	1.02	6.50
8. Bottom level—centre front	Fresh	0.67	6.40
9. Bottom level—against bottom	Bilgy—faecal	1.08	6.45
10. Bottom level—against back wall	Bilgy—faecal	0.92	6.40

SOUR FISH

During the spring and summer months a type of spoilage that was encountered very frequently had a succession of odours as follows: fresh→ seaweedy→ sour vegetables (mostly cabbage-like odours)→ sour kitchen drain→ putrid. Isolation and identification of the organisms responsible for these "sour vegetable" odours showed them to be chiefly green and blue-green

Pseudomonas. None of these organisms reduced trimethylamine oxide. Nevertheless, they must always have been accompanied by other organisms that did reduce this compound, because, except where pure cultures were used, the development of the odour was usually accompanied by a rise in trimethylamine.

"SWEET" AND "FRUITY" ODOURS

Another spoilage pattern, more often encountered in stored fillets but occasionally observed in gutted fish taken from the hold, was as follows: fresh → sweet (or perfume-like) → fruity → sour-fruity → sour-putrid → putrid. These "sweet", "fruity", and "sour" odours were also found to be produced chiefly by *Pseudomonas*, and the majority of the cultures isolated were non-pigmented. Those that were non-proteolytic developed only up to the sour-fruity stage, whereas similar, but proteolytic strains, carried the decomposition further, resulting in putrid fish. These organisms also did not reduce trimethylamine oxide. When sodium nitrite or some other agent which specifically inhibits the production of trimethylamine was added, the fish developed sour and fruity odours without any accumulation of trimethylamine. But under normal conditions, as the fish came from the boat, we never encountered strong-fruity or sour-fruity fish where the trimethylamine remained low.

TRIMETHYLAMINE AND INITIAL SPOILAGE ODOURS

It is remarkable that the relationship between trimethylamine and the development of the early spoilage odours is as close as it is. Trimethylamine is a volatile base, and the amount of free amine is dependent upon the pH. In the range of fresh to spoiling haddock (pH 6.3 to 7.5), there is a wide difference in the volatility of this amine and hence the intensity of odour that comes from a given concentration. It was found, for example, that with 20 ppm. trimethylamine added to buffered solutions, little or no odour was perceptible below pH 6.7. From 6.7 to 7.4 the odour became increasingly strong. At 6.7 to 6.9 this amount produced a characteristic "fishy" odour, while at 7.4 and above, it had the strong ammonia-like odour of the more concentrated amine.

Similar buffered solutions containing trimethylamine were left for 6½ hours in Conway dishes at 37°C. to determine the amount of volatile base taken up by a standard acid solution. Blanks gave readings of 0.96, 0.96, 0.97 ml. with N/35 sodium hydroxide. With trimethylamine added the results were:

pH		ml. N/35 NaOH
5.7 to 6.7	=	0.96 ml.
6.8	=	0.95
6.9	=	0.87
7.0	=	0.70
7.5	=	0.62

These tests, as stated above, were made with 20 ppm. trimethylamine, while the concentrations in the haddock were very much less. Even in the "smelly" fish, less than 25 per cent had pH values of 6.7 and above. Therefore it would seem obvious that during the early stages of spoilage trimethylamine may

accumulate in the muscle without contributing directly to the odours that are present; however, once the buffering capacity of the muscle has been overcome and the pH approaches neutrality, the accumulated amine will be freed and will then be a factor in the odours that are present. In spite of the fact that it does not contribute to the initial spoilage odours, the accumulation of this amine in the muscle appears to be a reasonably good measure of the total bacterial activity in this type of fish.

The Comparative Significance of pH and Trimethylamine Values in Cod

During the same period in which the haddock were being tested, 130 codfish were also examined for trimethylamine, pH and odour. Although this number was not sufficient for any final conclusions, it was enough to indicate a difference between the spoilage of cod and haddock. The cod had, for example, a higher initial pH range and the subsequent increase was much greater. The mean trimethylamine values were also higher for the cod, but the difference was not as marked as with the pH.

Although the same general relationships exist between trimethylamine, pH and odour for both haddock and cod, the significance of specific levels of trimethylamine and pH are not the same. The present limited data indicate that, for cod of comparable quality as determined organoleptically, the pH and trimethylamine values are higher than for haddock.

This suggests the need, not only for further work comparing cod and haddock, but also for similar studies with other commercial sea fish.

DISCUSSION

In this investigation it was found that with freshly incised haddock fillets the trimethylamine value was a more sensitive measure of the early stages of spoilage than either organoleptic rating or pH. On the other hand it was also shown that there is a very definite relationship between the development of early spoilage odours and the increase of trimethylamine. Once the muscle reaches a trimethylamine value of 1.0 mg. of trimethylamine N per 100 g. fish, it either has developed or will shortly develop a perceptible spoilage odour.

In theory, various types of bacterial spoilage could be produced without having a significant rise in trimethylamine. This can be demonstrated easily by using either pure cultures or enzyme inhibitors such as sodium nitrite. But under natural conditions it would appear that sufficient trimethylamine oxide-reducing bacteria are present to act as a measure of the activities of the total spoilage flora.

To this there was one marked exception: trimethylamine is *not* a measure of the type of spoilage that occurs in the so-called "bilgy" fish. This particular type of spoilage, incidentally, is the result, not of fish being contaminated by bilge water, but of certain types of bacteria growing on fish under anaerobic conditions. Although the number of bilgy fish may not always be of any importance from a statistical standpoint, the vileness and intensity of their odour

is sufficient to make them economically very undesirable. For this reason, any system of grading based on trimethylamine alone would have a serious weakness.

It should be emphasized that the results of this investigation apply to freshly filleted haddock that have been previously stored on ice; and furthermore, the organoleptic grading has purposely been very rigorous. A great many of the fish that have been rated as "not fresh" were still edible, and often in a better state of preservation than many fresh fillets obtainable in retail stores. The purpose here was not to separate edible from inedible fish, but to see whether it was possible to differentiate high quality fillets from those that were undergoing the initial loss in quality.

Other studies carried out at this station (which will be reported later) have shown that the trimethylamine levels for the various degrees of spoilage in the gutted fish are not the same for *stored fillets*. That is, the trimethylamine values that accompany initial spoilage odours are higher when spoilage develops through bacterial activity *after* the fillets have been cut out of the gutted fish, than when it occurs in muscle from freshly incised fillets. In the case of fillets that have been frozen and thawed, as well as of those treated with nitrite, we know that there may be no relationship between trimethylamine values and the degree of spoilage that develops.

Preliminary experiments have also indicated that, although the same general relationship exists between the increase in trimethylamine and the development of initial spoilage odours for both cod and haddock, the significance of specific levels of trimethylamine are not the same. The present limited data indicate that the trimethylamine values are higher for cod than for haddock of comparable quality as determined organoleptically.

This suggests the need, not only for further work comparing cod and haddock, but also for similar studies with both the freshly incised and stored fillets of other commercial fish.

Trimethylamine and the Spoilage Level of Stored, Frozen and Nitrite-Treated Fillets

Some related observations, not bearing directly on the thesis of this paper, should be borne in mind when the correlation of trimethylamine with organoleptic ratings of the muscle of cod and haddock is attempted.

FRESHLY CUT FILLETS VS. FILLETS HELD IN COOL STORAGE. In the whole gutted fish the principal spoilage takes place in the area of the gills, in the gut cavity and to a lesser extent in the slime on the exterior of the fish. Until spoilage is in an advanced state, the only products of bacterial activity that reach the muscle are those that diffuse in from locations where active decomposition is taking place (Lucke and Frercks, 1940; Dyer, Dyer and Snow, 1946). In the initial stages of spoilage, a relatively large percentage of the trimethylamine is on or near the surface of the fish, and therefore separated from the fillet during cutting, skinning and trimming. In contrast to this, let us examine what happens to a fillet that spoils during storage *after* it has been cut from the fish. Once again most of the

bacterial activity is on the surface, in this case the surface of the fillet. When this fillet is tested, there is no further cutting, trimming or skinning. The surface areas where most of the spoilage is taking place are included in the muscle tissue that is to be tested. For this reason, trimethylamine values of fillets that have been cut from good quality fish and spoiled during subsequent storage have not the same significance as trimethylamine values of freshly incised fillets. During this same period when studies were being made on the gutted fish taken directly from the vessels, a series of tests was made on fillets that were held in cool storage. Among other things, it was frequently observed that trimethylamine values of 4–10 were encountered in the stored fillets that had the same organoleptic ratings as freshly cut fillets with trimethylamine values of 1–1.5.

TRIMETHYLAMINE CONTENT OF FROZEN FISH. Pivnick (1949), Pottinger *et al.* (1952), and Hartshorne and Puncochar (1952) observed that trimethylamine values bore little or no relation to the rate of spoilage in fish or fillets that had been stored in the frozen state.

EFFECT OF NITRITE ON TRIMETHYLAMINE PRODUCTION. In Canada it is a common practice to dip fresh cod or haddock fillets that are to be used in the fresh fish trade in a weak solution of sodium nitrite. Under conditions where this salt has little or no effect on the growth and multiplication of the bacteria it may specifically inhibit their ability to reduce trimethylamine oxide to trimethylamine. The result is that very frequently nitrite-treated fillets are encountered that are spoiled without having any significant increase in trimethylamine.

One must be careful, therefore, in applying the data showing the significance of trimethylamine as a measure of spoilage for one type of fish to other fish or to similar fish under different environmental conditions.

SUMMARY

(1) From examining fillets cut from 850 iced haddock, it was found that trimethylamine was a more sensitive measure of early spoilage in fish muscle than either organoleptic examination or pH.

(2) At least one type of spoilage was encountered that was not accompanied by an increase in either trimethylamine or pH.

(3) Normally there is a close correlation between the development of most early spoilage odours and an increase in trimethylamine. For these haddock a trimethylamine value of 1–5 mg. per 100 g. indicated that the fish were already producing off-odours or would do so shortly.

(4) Trimethylamine is a useful measure of the initial spoilage changes in the fish muscle even though the trimethylamine itself may not contribute to the odours present.

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Some Physical Features of the Miramichi Estuary[1, 2, 3]

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ABSTRACT

The distribution of salinity, temperature and water transparency observed in the Miramichi estuary in 1950 and 1951 is correlated with the amount of precipitation, river discharge, wind velocity and other physical variables. Assuming complete mixing, the water exchange with the Gulf of St. Lawrence during a complete tidal cycle would be 15%. The residual or non-tidal circulation, resulting chiefly from river discharge, consists essentially of a seaward moving layer of drift within ten feet of the surface and a landward moving layer below that depth.

INTRODUCTION

During investigations on the ecology of barnacles in the Miramichi area in 1950 and 1951 (Bousfield, 1955) a considerable body of data on the distribution of salinity, temperature, water transparency and other physical features of the estuary was obtained. Limited observations of this kind had been carried on in the estuary during the Miramichi Fisheries Investigation of 1918 (Huntsman, 1945), by Rogers (1940), and more recently by field officers of the Fisheries Research Board of Canada. Changes in the shoreline and bottom topography have been studied (Cross, 1951) and a prediction of the circulation in the outer estuary has resulted from a recent tidal and current survey of the area (Fothergill, 1953). The present account utilizes this previous information in correlating observed changes in the distribution of salinity, temperature and water transparency with changes in precipitation, river discharge, wind velocity and other variables, and in predicting the residual or net water circulation in the estuary. The residual circulation predicted from the transport of barnacle larvae is in agreement with that herewith derived from physical considerations.

METHODS

A series of hydrographic stations was established inside the estuary proper and in the Gulf of St. Lawrence, in the immediate offing of the mouth of Miramichi Bay (Fig. 1). These stations were visited by means of a small motor boat at weekly intervals during the summer of 1951. A few stations had previously

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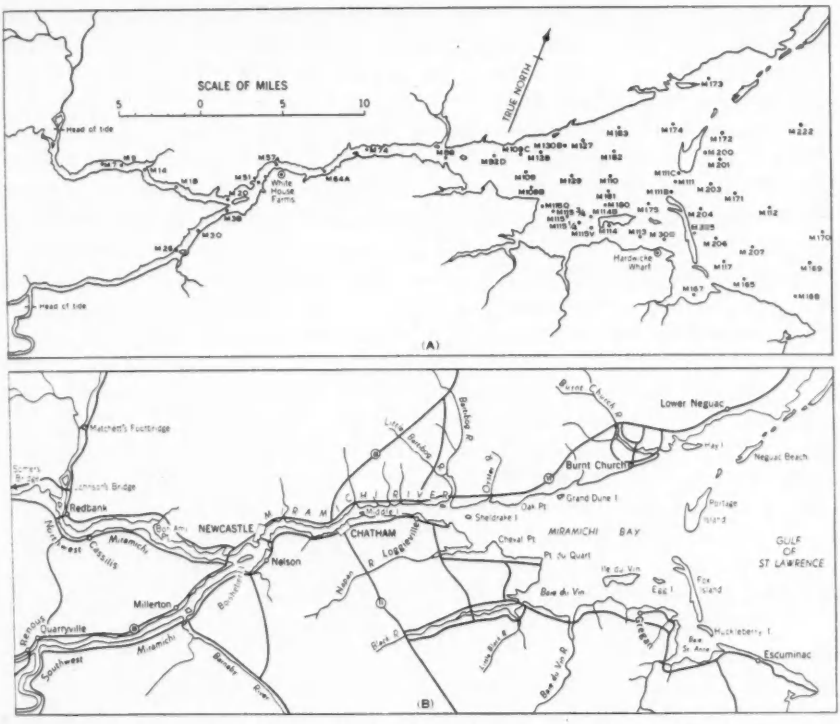


FIGURE 1. Topographical features of the Miramichi estuary: (A) Principal hydrographic stations, 1951; (B) Place names, rivers and roads (courtesy R. A. McKenzie, Chatham, N.B.).

been visited in August, 1950. Water samples for the measurement of temperature and salinity were obtained by means of a portable plankton pump. Bottom sediments were sampled by means of a small iron dredge and an Ekman bottom sampler.

Water temperatures accurate to the nearest 0.1°C. were taken using a mercury thermometer held directly beneath the outlet hose of the pump and read while completely immersed in the outflow. Heating or cooling of the water as it passed through the rubber intake hose and pump was found to be of small magnitude (0.0–0.1°C.), probably owing to the short length of hose exposed to both surface water and air temperatures and to the rapidity with which the water was pumped. The specific gravity of the sea water was determined by float hydrometer, and the salinity, accurate to one-tenth of one part per thousand, was calculated from Knudsen's Tables. Water transparency was approximated by the use of Secchi Disc. Wind direction and velocity were estimated in the Beaufort scale. Rough approximations of the velocity and direction of surface currents were sometimes made by timing the drift of the boat, and these values were substantially in agreement with the published information on tidal currents in this estuary.

Measurements of the discharge of the Miramichi River and several of its tributaries were undertaken at one period in 1950, and at three-week intervals during the summer of 1951. Since flow gauges at Blackville on the southwest branch (Fig. 2) had been discontinued in 1933, measurements of river flow at certain key locations in the main drainage basins were obtained in the following manner. A point in the river was selected where current velocity was at least one foot per second and the channel fairly regular. A wood chip was dropped in mid-stream and its passage over a measured distance of 100 feet timed. The

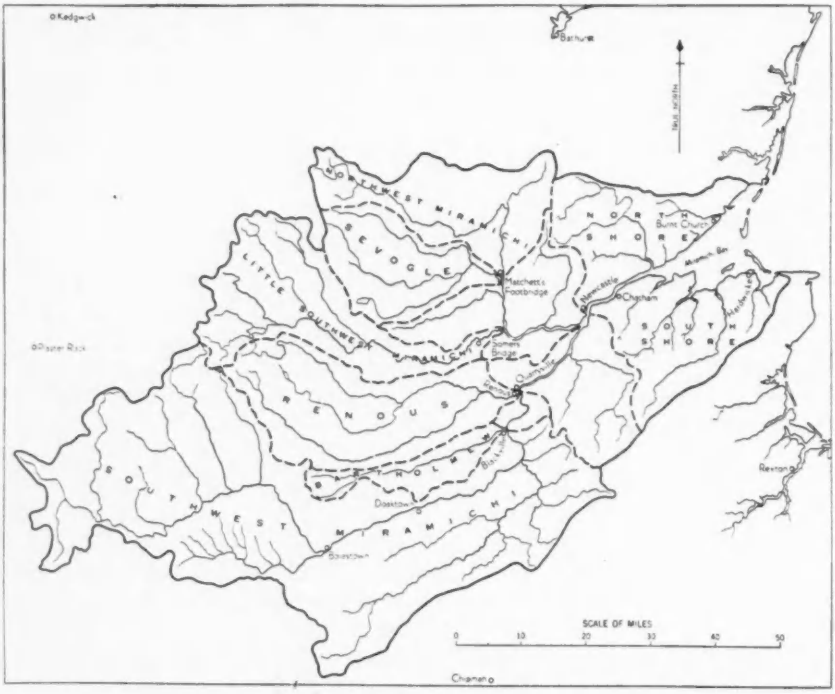


FIGURE 2. Principal drainage basins of the Miramichi watershed.

rate of flow was obtained from the average time of three such trials. The surface velocity obtained was then multiplied by the rapid stream factor of 0.9 to give the average speed of flow for the cross section. The average width and depth of the river at the site were measured by steel tape, and the discharge values then calculated (Tables III and IV).

Values for the daily and mean monthly discharge of the Southwest Miramichi River at Blackville, 1918 (Fig. 2), and for air temperature and precipitation were obtained from the last two sources cited under *Canada* in the list of references.

GEOGRAPHICAL FEATURES OF THE ESTUARY AND WATERSHED

Topographical Features

The Miramichi estuary is a large embayment of the east coast of New Brunswick, Canada, in which the entire surface drainage of the Miramichi watershed, 5,450 square miles in area, meets and mixes with the salt water of the Gulf of St. Lawrence (Fig. 2). The headwaters of the principal drainage basins, the Southwest Miramichi with its chief tributary, the Renous River, and the Northwest Branch with its chief tributary, the Little Southwest Miramichi River, rise a few miles east of the St. John River and flow eastward for nearly 100 miles to the heads of tide at Quarryville and Redbank, respectively. The total length of the estuary along the main channel from the head of tide in both branches to the mouth at Portage Island is almost 50 miles (80 km.). The inner or "river" portion of the estuary is formed by the tidal sections of the Northwest and Southwest Miramichi Rivers which merge just above Newcastle and, thus combined, flow eastward between sandstone cliffs to the river mouth at Sheldrake Island (Fig. 1). The outer or "bay" portion, into which drain several small tributaries of north and south shores, forms a triangle about 20 miles long from its western apex at the river mouth to its base at the eastern end. Miramichi Bay is cut off from the Gulf by a chain of sandy islands of which Neguac Beach, Portage and Fox Islands are the largest. Inside the bay are several lesser islands and sand bars of which Ile du Vin, situated two miles from the south shore, is the largest.

Submarine Physiography

The Miramichi is a shallow. coastal plain estuary. The average depth at lowest normal tides (datum of soundings) for the estuary, exclusive of the Neguac and Baie Ste Anne regions of water circulation (Fig. 10), is 13.0 feet. This figure was obtained from the average depth of segments, each one-tenth mile square, using navigational charts of the estuary. In the main channel the depth ranges between 20 and 50 feet, the average depth being about 25 feet (Fig. 3). The mean high-water depth of the estuary is 16.5 feet. The upper limit of the littoral zone, the tidal zone, occupies a vertical range of from five to six feet. From the mouth of the estuary, depths increase gradually in a seaward direction to the upper limit of the sub-littoral zone (165 feet) more than 25 miles offshore in the Gulf.

Bottom sediments in Miramichi Bay consist mainly of sand, mud or a mixture of both containing shells and small stones (Fig. 3). Deposits of pure sand extend in from the Gulf mainly along the north side as far west as Grande Dune Island, 8.5 miles above the mouth. Mud flats occupy much of the river bottom and inner bay. Sandy mud mixed with small stones, shells, eel grass and detritus are found mainly along the inshore shallows. Rocky outcrops, largely soft sandstone, are best developed near Point Escuminac but also occur inside the estuary at Point du Quart, Burnt Church, Oak Point, and upriver along the banks to Newcastle, 28.2 miles above the mouth. A few glacial till boulders, some

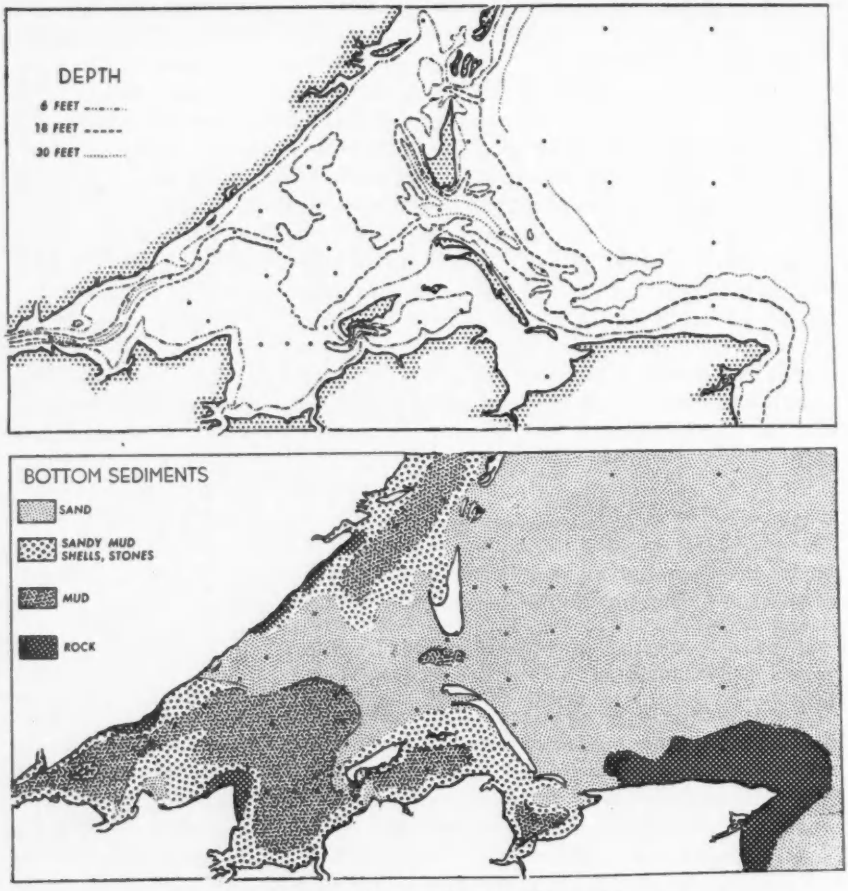


FIGURE 3. Submarine physiography of the Miramichi estuary.

of large size, are particularly conspicuous around Egg and Vin Islands, at Oak Point, and west of Napan Bay.

HYDROLOGY

RIVER FLOW

River discharge is a primary factor controlling the distribution of salinity and the magnitude of residual or non-tidal circulation in the estuary. The monthly mean values of river discharge have been estimated for the drainage basin above Newcastle, at the junction of the two main branches of the Miramichi River, and are given in Table I. Owing to the heavy annual precipitation (mean = 38.5 inches) and to the steep drainage gradients near the headwaters, the run-off

from the watershed is large. The estuary receives about nine-tenths of its fresh water from the watershed above Newcastle and the remainder from streams of the north and south shores below that point.

Following the break-up of river ice in mid April, the river discharge reaches an annual peak (28,000 cubic feet per second). As evaporation increases and the supply of melt-water decreases, the discharge decreases correspondingly to a minimum value late in August and early September (4,400 c.f.s.). A second smaller peak discharge occurs in November (9,000 c.f.s.). The winter minimum discharge (2,900 c.f.s.) is reached in February.

TABLE I. Monthly mean discharge of the Miramichi River at Blackville and Newcastle.

Month	River discharge (*cubic feet per second*)	
	Southwest Miramichi R. at Blackville (drainage basin of 1,950 sq. miles)	Miramichi R. at Newcastle (drainage basin of 4,500 sq. miles)
January	1,760	4,100
February	1,230	2,900
March	2,420	5,650
April	11,500	27,000
May	11,900	28,000
June	3,670	8,500
July	2,120	4,950
August	2,070	4,850
September	1,890	4,400
October	3,340	7,800
November	3,870	9,000
December	2,800	6,000

The estimation of the monthly values of river discharge at Newcastle (Table I) was based on two sources of data: (1) published river discharge measurements at Blackville, Southwest Miramichi River, for the years 1918–33, and (2) present river discharge measurements at the junctions of the main tributaries just above the head of tide. Both sets of data may be compared by expressing them in terms of the monthly mean discharge per unit area (c.f.s. per square mile) for the individual drainage basins concerned. The surface areas of component drainage basins and the total area of the Miramichi watershed are given in Table II. The areas are given, for convenience, above points at which discharge measurements were taken.

The run-off per unit area during the summer is similar in all drainage basins above Newcastle, and therefore the run-off from a given basin may be assumed directly proportional to its area. The river discharge at Newcastle is thus 2.3 times that of the Southwest branch above Blackville, as shown in Table I. The drainage per unit area was derived mainly from measurements of river discharge during the summer of 1951 at selected stations above Newcastle (Table III) and below Newcastle to the Gulf (Table IV). Based on five sets of observations on

TABLE II. Drainage areas of the principal drainage basins of the Miramichi watershed. (Measured by planimeter from Canadian Topographic Sheet 21 N.E.)

Drainage basin	Area
	sq. miles
Southwest Miramichi R. (above Blackville)	1,945
Southwest Miramichi R. (Blackville to Newcastle exclusive of the Renous)	445
Renous R. (above Quarryville)	580
Total Southwest Miramichi R. (above Newcastle)	*2,970*
Northwest Miramichi R. (above Matchett's footbridge)	390
Big Sevogle River (above Matchett's footbridge)	310
Little Southwest Miramichi R. (above Somer's Bridge)	495
Northwest Miramichi R. (remainder above Newcastle)	330
Total Northwest Miramichi R. (above Newcastle)	*1,525*
Total Miramichi drainage basin at Newcastle	**4,495**(4,500)
North Shore rivers (below Newcastle)	395
South Shore rivers (below Newcastle)	435
Miramichi Bay	120
Total drainage area below Newcastle	**950**(950)
Total Miramichi watershed (at Portage Island)	**5,445**(5,450)

four drainage basins above Newcastle, the average summer discharge per square mile, for all rivers combined (80% of the total drainage area above Newcastle), was 1.3 c.f.s. The values for both Northwest and Southwest branches agree with this closely, whereas those of the Renous and Little Southwest differ from it by 25%, probably owing to local variations in run-off from day to day when the measurements were made. The average summer discharge of the Southwest branch at Blackville over the 15-year period, 1918–33, was also 1.3 c.f.s. per square mile. As the drainage area of the Southwest branch is nearly one-half that above Newcastle (Table II), the unit discharge of the Southwest branch is thus probably representative of the entire watershed. The estimated mean monthly discharge values for the watershed above Newcastle are therefore 2.3 times greater than the corresponding values at Blackville, as shown in Table I.

The remainder of the Miramichi watershed (that below Newcastle) is composed of north and south shore tributaries having approximately equal drainage areas. Combined, these make up less than one-sixth of the total Miramichi drainage area. The combined discharge of north shore rivers during August (Table IV) was almost twice that of south shore rivers. This difference may be attributable to differences in precipitation, subsurface drainage, and steepness of gradient between the relatively swift north shore rivers and the low-lying slower moving peat bog streams of the south side. During August, the unit discharge of these tributaries combined is approximately 0.6 c.f.s. per square mile, whereas that of the main part of the Miramichi watershed above Newcastle is 1.0 c.f.s. per square mile (Table III). The total run-off from the north and south shore basins is therefore only one-tenth ($\frac{1}{6} \times 0.6$) that of the total Miramichi watershed, and its influence on estuarine salinities, relative to that of the main river, is small.

TABLE III. Measured discharge of tributaries of the Miramichi River, N.B., during 1950 and 1951.

Drainage basin	Drainage area above point of measurem't	Measured discharge					Total discharge (5 dates)	Average ratio of discharge to area
		1950	1951					
		Aug. 17	June 6	July 10	Aug. 2	Aug. 28		
	sq. miles	*c.f.s.*	*c.f.s.*	*c.f.s.*	*c.f.s.*	*c.f.s.*	*c.f.s.*	*c.f.s./sq. mi.*
Northwest Miramichi (above Matchett's)	391	160	1,310	555	390	165	2,580	1.32
Little Southwest Mir. (above Somer's Bridge)	497	340	1,600	800	850	410	4,000	1.61
Renous River (above Quarryville)	580	180	930	730	620	480	2,940	1.02
Southwest Miramichi (above Quarryville)	2,100	1,600	5,130	3,200	2,160	1,800	13,890	1.32
Total	3,568	2,280	8,970	5,285	4,020	2,855	23,410	
Mean discharge/sq. mile					*1.0*			*1.3*

TABLE IV. Measured discharge of tributaries of the lower Miramichi River and Bay.

Stream	Site of discharge measurement	Date (1951)	Time (A.D.S.)	Temp. (°C.)	Discharge (c.f.s.)
NORTH SHORE TRIBUTARIES OF THE MIRAMICHI RIVER BELOW NEWCASTLE, N.B.					
French Fort Creek	Detour highway bridge	Aug. 10	2:00 p.m.	12.5	15
Stewart Brook	At highway culvert	Aug. 10	2:00	12.9	1
Douglastown Stream	Above highway bridge	Aug. 10	3:00	15.6	2–3
McKeown Stream	Highway culvert	Aug. 10	3:00	...	1
Stothart Stream	Highway culvert	Aug. 10	3:00	...	1
Goodfellow Stream	Highway culvert	Aug. 10	3:00	...	2
Hamilton Brook	Highway culvert	Aug. 10	3:15	16.9	6
Big Brook	Highway culvert	Aug. 10	3:15	...	1
Gordon Brook	Highway culvert	Aug. 10	3:15	...	1
Little Bartibog R.	Below bridge (Hwy. 8)	Aug. 10	4:00	17.7	70
Big Bartibog R.	At Bartibog Bridge	Aug. 10	4:30	18.3	160
Oyster River	At Highway #11	Aug. 15	2:00	19.0	9
Burnt Church R.	At Highway #11	Aug. 15	4:45	19.1	41
Total discharge, N. shore rivers					*315*
SOUTH SHORE TRIBUTARIES OF THE MIRAMICHI RIVER BELOW NEWCASTLE, N.B.					
Napan River	At Highway #11	Aug. 17	7:30 p.m.	...	8
Black River	At Highway #11	Aug. 17	7:45	...	12
		Sept. 2	3:55	17.9	23
Little Branch R.	Old Planing Mill	Sept. 2	4:30	...	8
Harton's Creek	At Shore Road	Sept. 2	4:50	...	9
Baie du Vin R.	Buckley's Bridge	Sept. 2	2:15	17.5	55
MacInnis Creek	At Shore Road	Sept. 2	1:15	...	13
Dennison's Creek	At Shore Road	Sept. 2	1:00	...	7
French Brook	1 mile above H'dw'ke	Aug. 27	6:00	18.0	2/3
Meadow Brook	W. Branch Eel R.	Aug. 27	4:40	18.0	1
Scofield Brook	Eel River	Aug. 27	5:00	19.3	2¼
Eel River (combined)	Thiereau's Bridge	Aug. 27	3:30	20.5	26
Portage River	East Branch (Junction)	Aug. 27	4:00	20.2	7½
	West Branch (Junction)	Aug. 27	4:00	18.3	
Savoy Brook	Road at Baie Ste Anne	Aug. 27	4:30	25.0	½
Total discharge, S. shore rivers					*160*

RELATION OF RIVER FLOW TO PRECIPITATION

A comparison of available data for the daily river discharge during the summer and fall of 1918 with the corresponding data for daily precipitation (Fig. 4) shows that the river discharge is closely related to precipitation over the entire watershed, that peak river discharge normally occurs within two days of peak precipitation, and that prolongation of high or low periods of surface run-off depends upon the duration of the rainy or dry spell, respectively.

A comparison of total monthly precipitation and corresponding monthly mean river discharge at Blackville for the years 1918 to 1933 shows in general that the monthly mean value of river discharge tends to be proportional to the

total precipitation of the same month. The relationship appears to be strongest during the summer and fall, but weakest in the spring. The prediction of monthly mean discharge values based solely upon the total monthly precipitation is not dependable, except within wide limits, however, owing to lag run-off from precipitation of previous months, to seasonally variable evaporation, and in the spring, to lag run-off from melting snows.

On the basis of the above relationships it is possible to predict from precipitation data alone that the river discharge was below normal during the spring and summer of 1950, but was abnormally high during comparable periods of 1951 (Fig. 4).

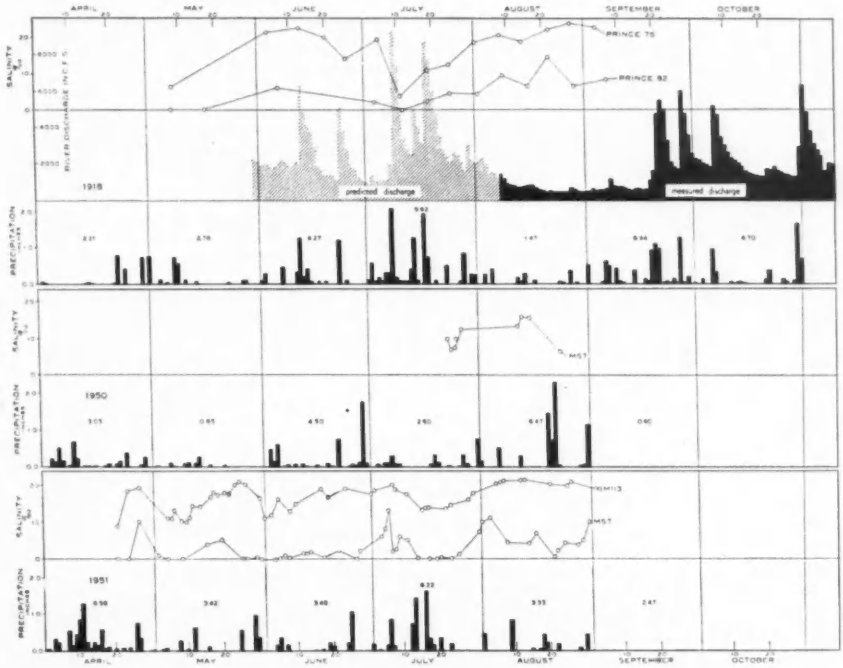


FIGURE 4. Daily and total monthly precipitation at Chatham, N.B. during spring and summer months, 1918, 1950 and 1951, showing corresponding fluctuations in the measured and predicted discharge of the Southwest Miramichi River at Blackville, 1918, and in the surface salinity at stations in the Miramichi River below Newcastle (*Prince* 82, M57) and in Miramichi Bay at Vin Island (*Prince* 75, M113) 1918 and 1951.

HYDROGRAPHY

Water temperature, salinity, transparency and general meteorological conditions of the Miramichi estuary were measured at weekly intervals during the summer of 1951, and the "normal" pattern of each of these variables was deter-

mined. Variations in the typical pattern of salinity, temperature and transparency were related to abnormal river flow and wind velocity.

Salinity

The horizontal distribution of salinity in the river and bay portions of the Miramichi estuary are shown in Figures 6 and 7 respectively. The horizontal distribution of salinity ranges from fresh water (0‰) at the head, to an almost marine environment (salinity 20–27‰) at the mouth. Surface salinities are normally less than 3‰ in the river above Boishebert Island (M20), less than 10‰ above Sheldrake Island (M88), and less than 23‰ above Portage Island (M111). The steepest horizontal gradients of salinity are about 1‰ per mile, and are

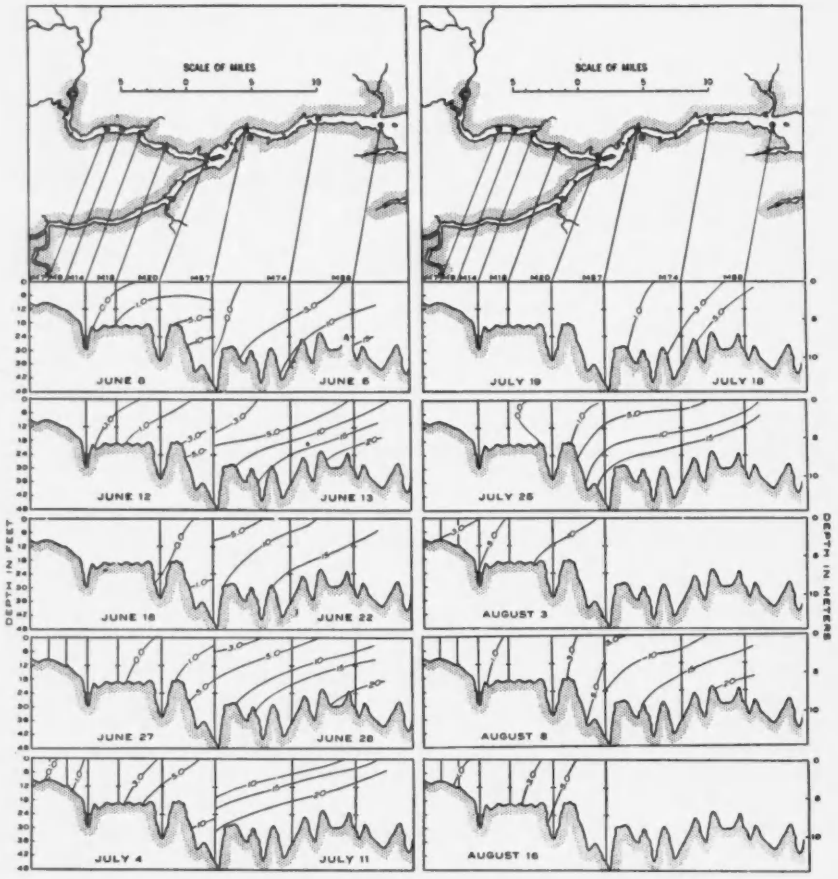
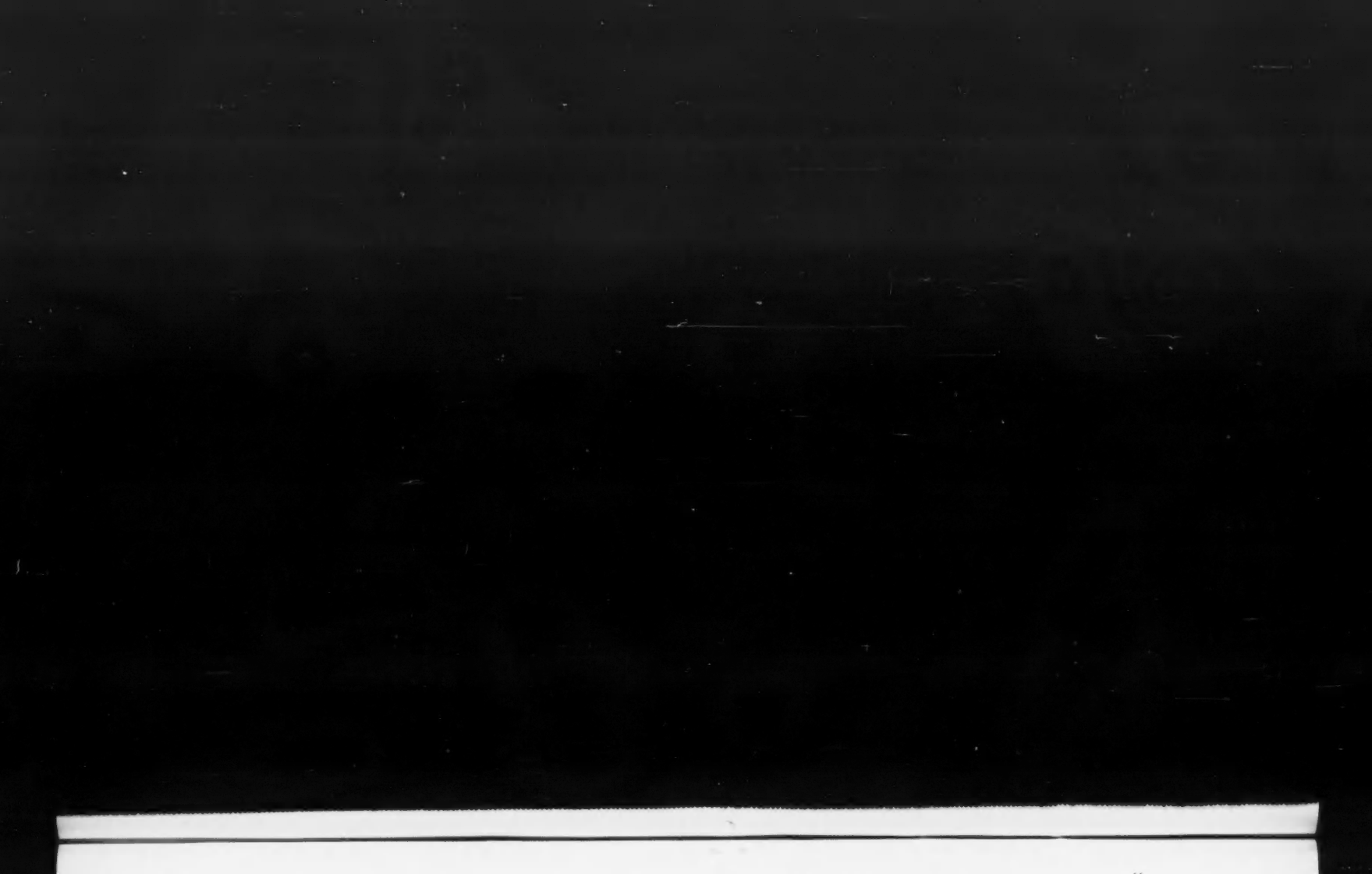


Figure 5. The distribution of salinity (‰) in the river portion of the Miramichi estuary at weekly intervals during June, July and August, 1951.



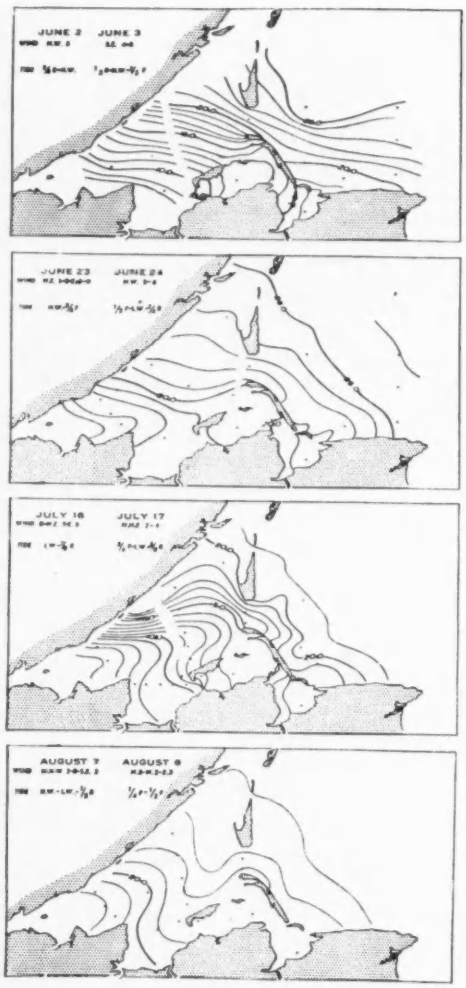
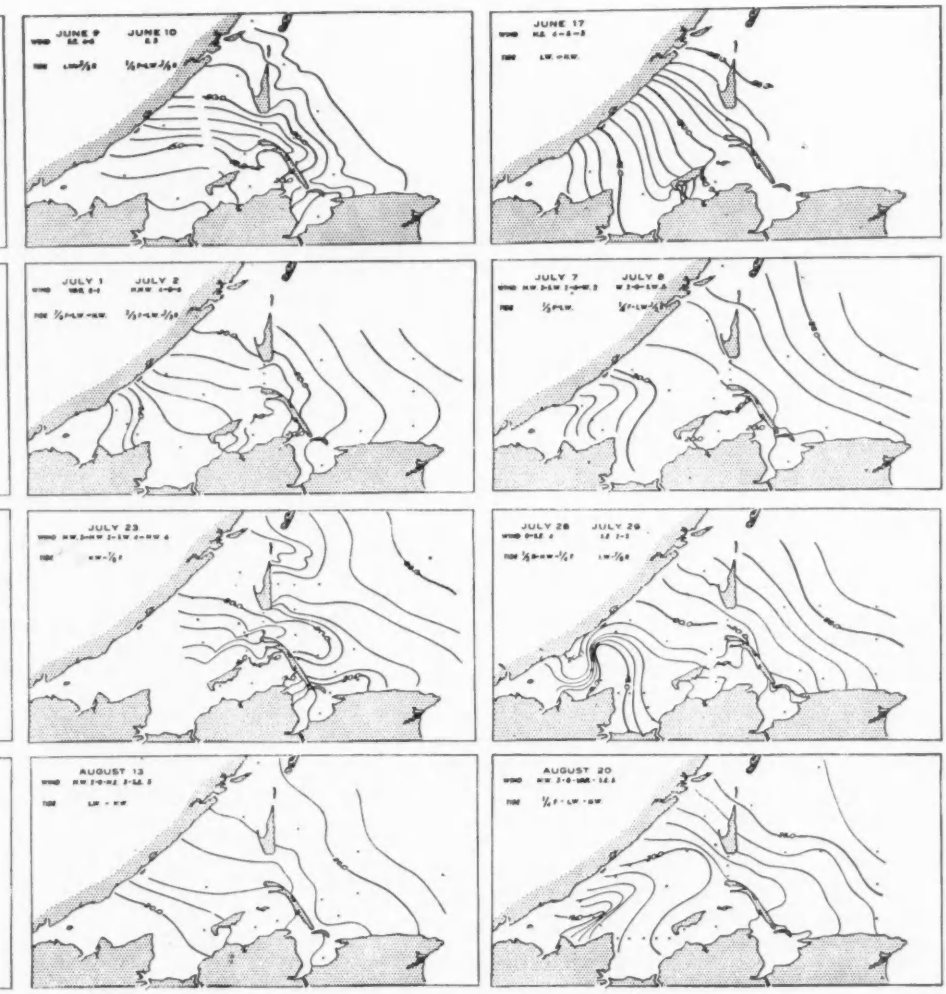


FIGURE 6. The surface distribution of salinity



of salinity (‰) in Miramichi Bay at weekly intervals during June, July and August, 1951.

located near the river mouth (Fig. 5). The difference in salinity between high and low water at a given location is about 2–3‰ and seldom more than 5‰. The surface isohalines in the bay (e.g. on June 2 and 3) slant diagonally across, rather than perpendicular to, the principal longitudinal axis of the estuary, owing to the effect of the earth's rotation on the circulation.

Strong vertical gradients of salinity are normally present, as illustrated by the sections along the river channel (Fig. 6). The difference in salinity between surface and 24 feet (near the bottom) is greatest near the river mouth (more than 10‰), and least (less than 1‰) near the landward limit of salt water in the river, and offshore in the Gulf. The seaward flow of fresh water at the surface, and the landward counter-drift of salt water along the bottom, maintain the salinity stratification in spite of strong mixing action by tidal currents and at times by the wind.

Variations from the assumed normal pattern of salinity distribution were most pronounced on July 16 and 17 in the bay (Fig. 7) and on July 18–19 in the river (Fig. 6). Salinities were abnormally low at this time owing to the prolonged heavy precipitation and heavy freshets during the week of July 12–18. The effect of the wind is most clearly shown in the bay on June 17 when a strong onshore wind upset the assumed normal pattern. The offshore wind of July 23 reinforced the seaward drift at the surface and created an upwelling of salt water in the lee of Portage and Fox Islands.

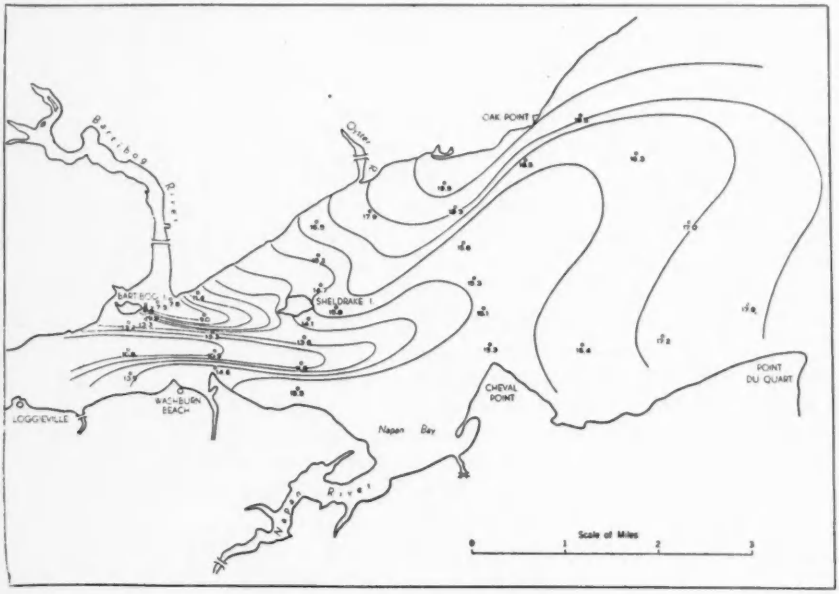


FIGURE 7. Surface salinity at the mouth of the Miramichi River, August 30, 1951. Time–10:12 A.M.–1:15 P.M. (A.D.S.T.). Wind SE 1–2, Tide ¾ F.–LW.

A general increase in salinity during June and early July is shown in Figures 6 and 7. During this period, river flow decreased markedly as the spring meltwaters disappeared and evaporation increased. Salinities became higher again during August.

The surface salinity at river station M57 and bay station M113 during the summer of 1951 and part of July and August, 1950, may be related to the corresponding precipitation as shown in Figure 4. Salinities at both stations were exceptionally low following heavy precipitation in mid-April, at the end of May, and in mid-July, and in late August in 1950. Surface salinities at equivalent stations of the Miramichi Fisheries Expedition in 1918 (also Fig. 4) show a corresponding drop during exceptional precipitation and river discharge in July, and a return to normal during dry weather as in August. In absence of salinity data for much of 1950, it is probable, therefore, that the upriver penetration of salt water in that year was much greater and remained so for longer periods than that in 1951. Thus, in May, June and July of 1950, precipitation and river discharge were much below normal, salt water probably reached its extreme possible limit of penetration upriver, and probably remained at this level during most of the summer. In 1951, however, precipitation and river discharge were much higher than normal and salt water was very largely restricted during much of the summer to the region below Boishebert Island.

Water Temperature

Except during winter the annual cycle of water temperature in the Miramichi estuary parallels that of the air. From mid-November to April 1, average air temperatures are below the freezing point and reach a minimum of 10–15°F. during February. The winter freeze-up in the river lasts from December 1 to mid-April and the ice reaches a thickness of about two feet. The water warms rapidly during May and June and summer surface maxima of 18–22°C. are reached in July and August. It cools rapidly during October and November to the freezing point in December. During the summer of 1951 the average air temperature and the average water temperature were about 1°C. and 2°C., respectively, above that of 1950.

The surface distribution of temperature in the bay part of the estuary is shown in Figure 8. During the summer, the surface waters of the river and bay are usually 1–2°C. warmer than those of the Gulf immediately off the mouth of the estuary. Surface temperatures of the south side of the outer estuary (bay) are warmer than those of the north side owing to the influence of the Coriolis acceleration on the circulation. Freshets temporarily decrease surface temperatures as shown on July 16 and 17. Strong onshore winds tend to equalize temperatures throughout the estuary, as on June 17, and offshore winds create an upwelling of cold water in the lee of the land, as on July 23.

A perceptible thermocline is usually present, particularly when the corresponding halicline is well marked. Surface temperatures are often 2–3°C. higher than those at a depth of 25 feet (bottom). Diurnal variation in surface tempera-

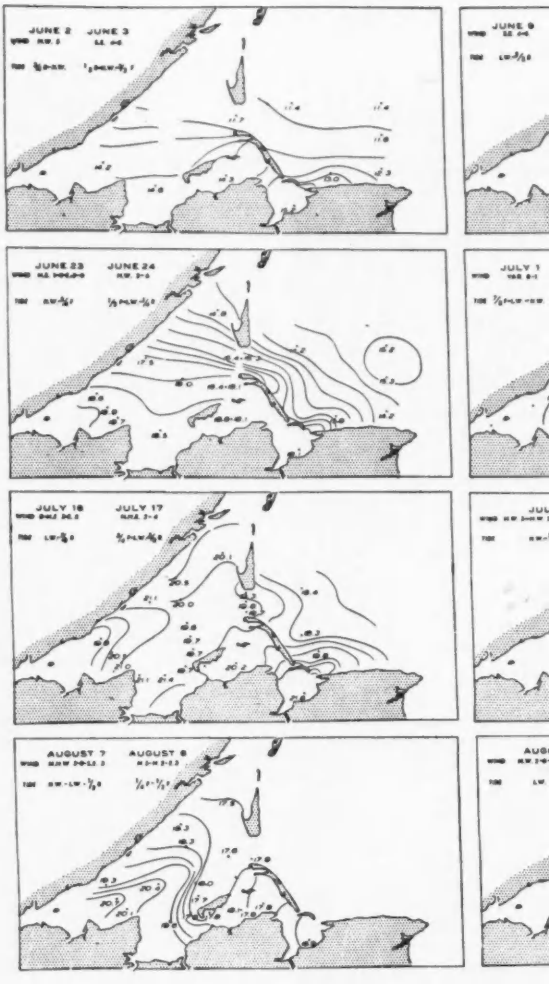
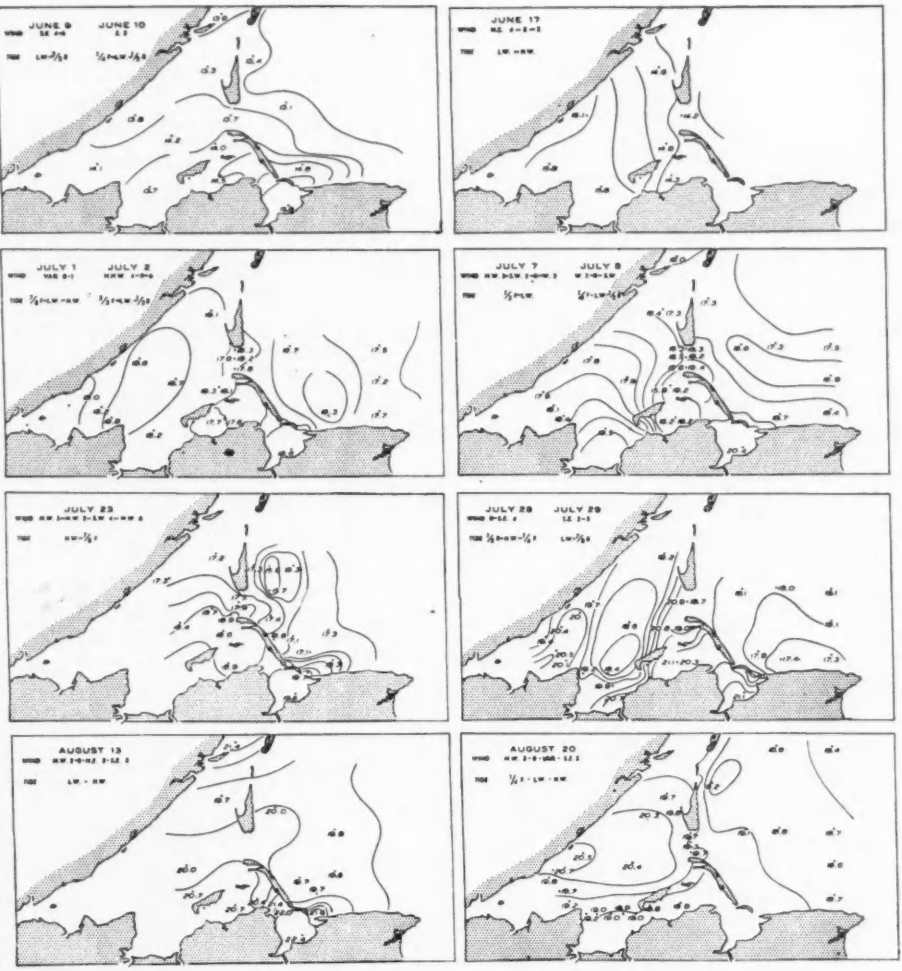


FIGURE 8. The surface distribution of temperatur



emperature (°C.) in Miramichi Bay at weekly intervals during June, July and August, 1951.

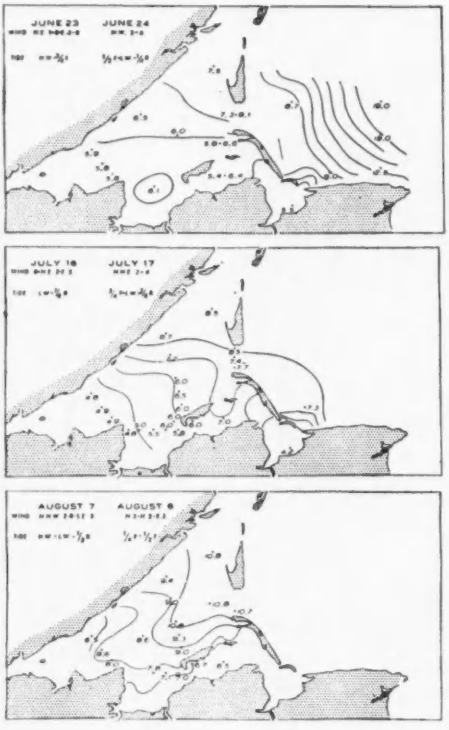
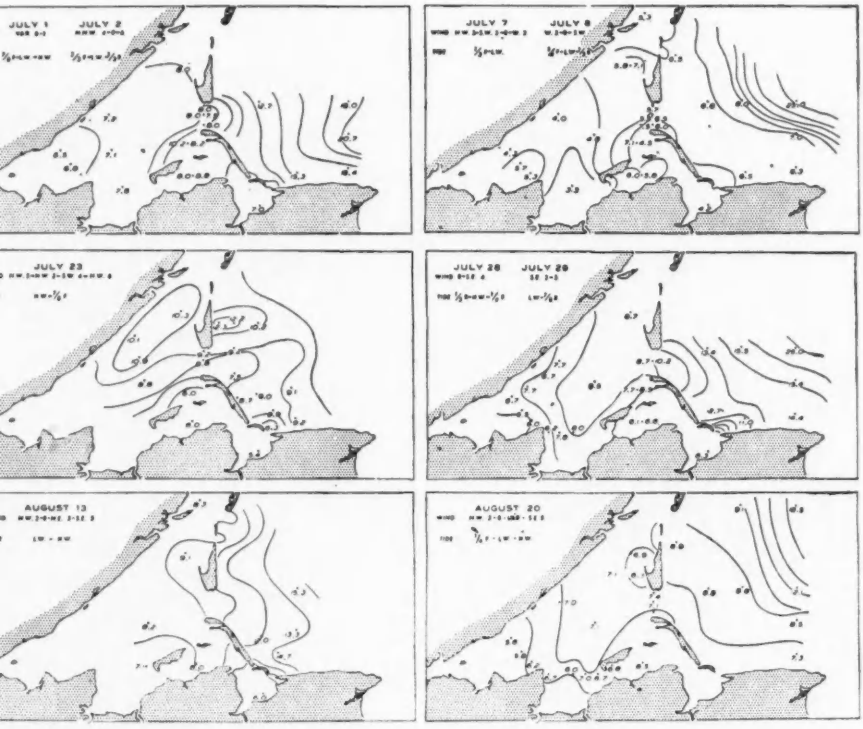


FIGURE 9. The distribution of water tra



water transparency in Miramichi Bay during June, July and August, 1951.

ture in summer is about 2°C; variation resulting from tidal ebb and flow is probably less than 1°C. (see Fig. 11, diagram A).

Water Transparency

The distribution of water transparency in the Miramichi estuary at weekly intervals during the summer of 1951 is shown in Figure 9. Transparency inside the estuary is normally much less (Secchi Disc = 6 to 8 feet) than that of the Gulf of St. Lawrence (S.D. = 20 feet). The low transparency in the estuary proper is attributable to the influx of turbid river water, which also shows a brown stain during exceptionally heavy run-off, to the stirring up of bottom sediments by tidal currents and winds, and probably also to the population of phytoplankton and zooplankton. The headwaters and south side of the bay are normally less transparent (S.D. = 6 feet) than those of the outer bay and north side (S.D. = 8 feet) owing to the influence of the earth's rotation on the circulation. Abnormally low transparencies were observed on July 7 and 8 and August 20, following strong winds, and on July 16 and 17, following exceptionally heavy river discharge.

Tidal Currents

The most conspicuous feature of the circulation in the Miramichi estuary is the oscillating seaward and landward movement of the water associated with the rise and fall of the tide. The mean rise of tide above datum (Portage Island) during the summer is 3.5 feet (Tide Tables, 1951). At Cassilis, near the head of tide on the Northwest branch, high water occurs 1½ hours later and low water 3 hours later than at Portage Island.

The tidal curve varies over a period of two weeks from a regular semi-diurnal curve with two equal high waters and two equal low waters in each day to an almost pure diurnal curve, with only one clearly defined high water and a prolonged stand at low water (Cross, 1951.) The basic data for the direction and velocity of tidal currents in the outer estuary (Fig. 10) have been obtained from nautical charts and field observations, corrected to the results of Fothergill (1953). Surface currents of 1½–3 knots are encountered at the entrance to the bay and in the river during mid-flood and mid-ebb. Surface velocities tend to be somewhat higher and of longer duration on the ebb than on the flood owing to the river flow.

Related to the openings from the estuary into the Gulf of St. Lawrence, there are four principal regions of water circulation, as demarcated by the interrupted lines in Figure 10. On the flood, the main body of water passes in from the Gulf between Portage and Fox Islands, across the bay, and thence on up the river. On the ebb the reverse seaward movement across the bay takes place. The data of Fothergill (1953) on the velocity of tidal currents provide further evidence that the landward movement on the flood is strongest on the north side, and the seaward movement on the ebb is strongest on the south side of the estuary. Lesser tidal exchanges take place north of Portage Island (Neguac Gulley), through the

south side of the main entrance and around Vin Island, and directly from Baie Ste. Anne through two small passages on either side of Huckleberry Island. The demarcation between the main outflow and that of the south side may appear, as on July 23, as a line of white foam or "tide rip" at the surface, accompanied by marked differences in salinity, temperature and water transparency on either side of the line (see Fig. 7, 8, 9). However, considerable mixing and overlapping

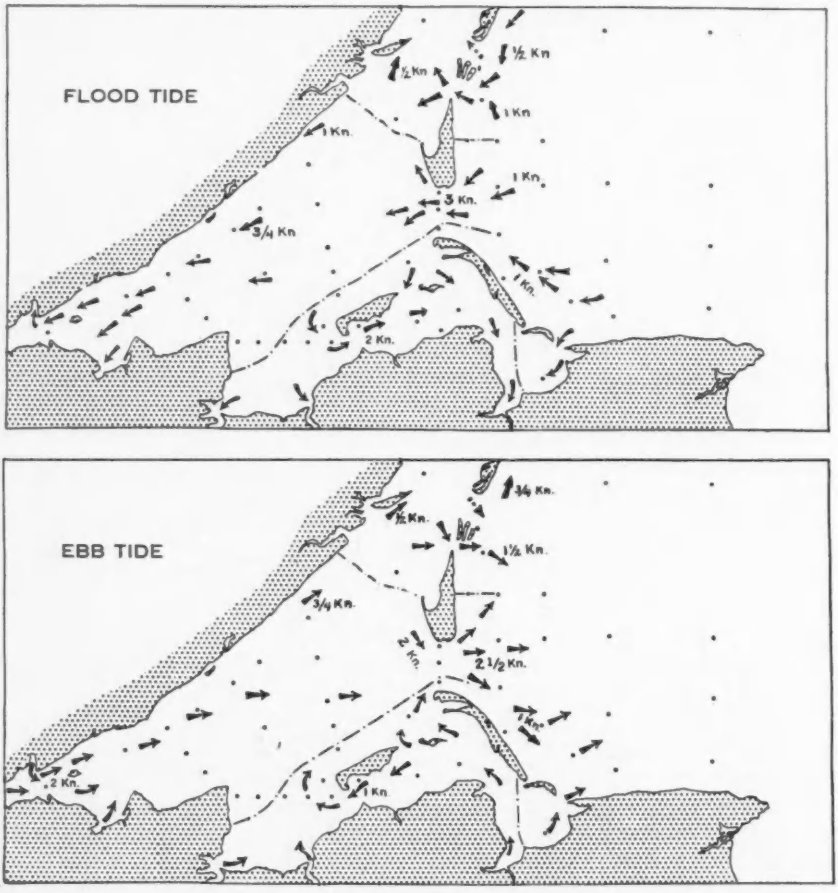


FIGURE 10. Surface tidal currents in the Miramichi estuary.

of the main water mass with that of the south side of the bay usually takes place between Portage and Fox Islands at the mouth. Mixing appears to be strongest in the bay where action of the wind augments that of the tide.

For the prediction of the distribution of salinity, and also plankton, it is useful to know what proportion of estuarine water is carried out of the estuary

and is exchanged with Gulf waters during each tidal cycle. Assuming complete mixing the amount of tidal exchange with the Gulf may be approximated from the exchange ratio, *r*, having the value

$$r = \frac{P}{P + V}$$

where P is the intertidal volume of the estuary and V the low tide volume (Ketchum, 1951). Assuming the surface area at high water equal to that at low water, P may be represented by the mean rise of tide, and P + V by the mean depth at high water. Owing to the diurnal inequality in the rise and fall of tides in the Miramichi area, the mean tidal difference, in this instance 2.4 feet, may be used for P. The mean depth at high water for the estuary is 16.5 feet (13.0 + 3.5 feet). Substituting values, *r* becomes 2.4/16.5 = 0.15 (approx.). On the above assumptions, therefore, the proportion of water moving seaward during each tidal cycle, which does not return on the following flood, would be approximately 15%.

The Residual or Non-Tidal Drift

Owing to inequalities in the velocity and duration of tidal currents set up principally by river discharge, the residual or net displacement of water through any complete cross section of the estuary during a complete tidal cycle is in a seaward direction. The fresh water of the river, being of lower specific gravity than salt water, tends to remain near the surface. As a result, the seaward drift takes place near the surface. The salt water entrained with the fresh (as brackish water) on its seaward movement at the surface is replaced by means of a residual landward counter-drift of salt water along the bottom.

The direction and velocity of the non-tidal drift at various depths in the Miramichi estuary may be obtained in two ways. The first way is by direct measurement of tidal velocities over a continuous series of tidal cycles according to the procedure of Pritchard (1952). Such measurements however were not obtained during the present investigation. The second way is by analysis of the vertical distribution of salinity throughout a complete tidal cycle at several reference stations throughout the estuary.

The effect of the circulation on the vertical distribution of salinity is indicated by measurements of salinity at six-foot intervals from surface to bottom at river station M57, at two-hour intervals during a complete tidal cycle (Fig. 11, diagram B). Temperature changes (diagram A) also illustrate the difference in hydrographical conditions at this station between high and low water and between day and night (p. 354). Salinities were lowest at low water (at both surface and bottom) but were highest at the bottom at high water, and at the surface at mid-flood and mid-ebb. This last observation implies that tidal mixing is greatest when tidal velocities are greatest. Little change in salinity took place in the halicline (about 12 feet in depth) during the complete tidal cycle.

The observations on the salinity cycle also suggest that the circulation in the Miramichi is like that in the Chesapeake estuarine system studied by Pritchard (1952). In the Chesapeake system, the velocity of non-tidal drift is maximal in

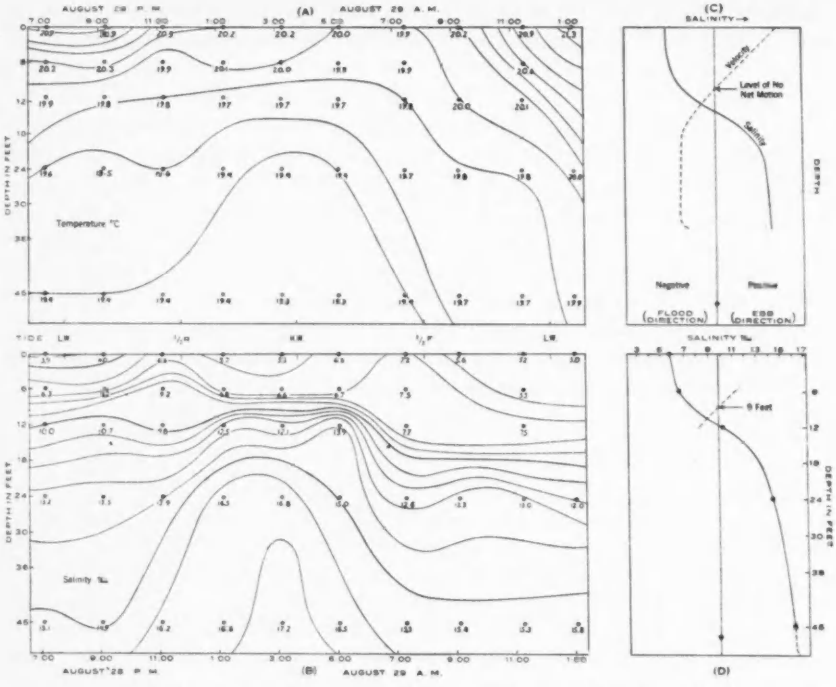


FIGURE 11. Changes in temperature and salinity with depth at Miramichi River station M57 during one complete tidal cycle: (A) temperature; (B) salinity; (C) characteristic salinity and net velocity vs. depth curves for a typical coastal plain type estuary (after Pritchard, 1951); (D) salinity vs. depth curve for one complete tidal cycle; average of salinity values of D showing the estimated level of no net motion.

a seaward direction at the surface and in a landward direction near the bottom, and minimal at some intermediate depth (the level of no net motion), as illustrated in Figure 11, diagram C. The net drift maintains a steady-state vertical distribution of salinity which takes the form of an inverse tangent function. Pritchard (1952a) has proposed a mathematical relationship for the prediction of the net velocity vs. depth curve from the corresponding salinity data provided mean tidal velocities at reference stations in the estuary are known. For the present, it may be noted that the level of no net motion occurs above the inflection point in the generalized salinity curve (diagram C) a distance approximately equal to one-quarter the total depth of the inflection point. In the Miramichi estuary, a strikingly similar salinity curve was obtained by averaging the salinities over the tidal cycle (diagram B). This curve is shown in diagram D. The inflection point of the salinity curve is about 12 feet in depth. The level of no net motion at this station would therefore be about 9 feet in depth, as indicated.

This level, estimated from the results of only one such series of measurements over a complete tidal cycle, is probably close to the average value for the entire estuary.

The level of no net motion tends to vary somewhat throughout coastal plain estuaries, such as the James estuary (Pritchard, 1952a). As a result of more recent experiences in similar estuaries, that author (personal communication) would conclude that in the Miramichi estuary above Sheldrake Island there is most likely a downstream movement of the upper layer of water and an upstream net flow of the deeper layer with the boundary between these two layers having a depth of about 7 feet on the NNW (left) shore and about 11 feet on the SSE (right) shore. The slope of the boundary is related to the effect of the earth's rotation. In the wider segment of the Miramichi estuary below Sheldrake Island the slope of the boundary between the upper layer of downstream flowing water and the lower layer having a net upstream flow becomes more marked, to the extent that it probably intersects the surface. In this region there is (to be expected) a central segment running longitudinally along the estuary in which downstream-flowing water overlies the upstream-flowing water. However, there would be a considerable segment of the right side of the bay in which downstream-flowing water extends to the bottom, and a considerable segment on the left-hand side where upstream-flowing water extends to the surface. Exchange between the lower salinity downstream-flowing water and higher salinity upstream-flowing water takes place laterally as well as vertically in the wider portion of the estuary, but occurs primarily in the vertical plane in the section above Sheldrake Island. The average level of no net motion in the Miramichi estuary would probably be of the order of 10 feet in depth.[5]

The resultant transport of larval stages of the brackish water barnacle *Balanus improvisus* during its 18-day planktonic life period supports the present estimate for the level of no net motion (10 feet in depth). The first three nauplius stages, occurring mainly above the 10-foot level, are transported successively seawards. The fourth and fifth stages, found at or slightly below this level, are concentrated near the mouth of the estuary; whereas the sixth-stage nauplius and the cyprid, occurring mainly below 10 feet in depth, are carried progressively landward towards the head of the estuary (Bousfield, 1955). Also, the earlier stages are concentrated on the right hand side of the outer (wider) portion of the estuary, whereas the later stages are mainly on the left side. If all larval

[5]According to Pritchard (personal communication) ". . . in [estuarine] systems dominated by return bottom flow, the boundary between the seaward directed flow and the landward directed flow occurs at close to middepth. In a natural estuary the meaning of middepth is somewhat obscure and our experience shows that the depth of the surface of no net motion lies somewhere between half the average depth of the cross section and half the channel depth. From the figures given [see page 345 above] the average depth of the Miramichi estuary is slightly less than 15 feet and the channel depth averages about 25 feet. Thus, the average depth of the surface of no net motion would be between 7½ feet and 12½ feet. An inspection of the shape of the vertical salinity profile [fig. 11, above] further confirms this suggested depth range."

stages tended to maintain a uniform vertical distribution, tidal exchanges with the Gulf during this period (exchange ratio of 15% per tidal cycle) would deplete the larval population below the level necessary to maintain the adult population on the bottom. The relation between the depths at which the successive larval stages drift and the estuarine circulation (above) is the mechanism by which the barnacle population is maintained near the head of the estuary.

The net drift at various depths in the Miramichi estuary may be estimated on the assumption that Pritchard's relationship between tidal velocities and non-tidal drift derived from studies in the James estuary is applicable here. The assumption is partly justified by the close degree of similarity between the Miramichi and James estuaries in size, depth, tidal range, river discharge and direction of flow. The drift velocities cannot as yet be calculated from the salinity equation of Pritchard (above), since even the most recent tidal studies in the Miramichi area (Fothergill, 1953) do not give sufficiently adequate mean tidal velocities for reference stations in the area. However, Pritchard (1952a) has shown that, in the James estuary, the mean non-tidal velocity in both upper and lower water layers is approximately one-fifth the magnitude of maximum tidal current velocities at those depths. At Miramichi River station M57 the maximum surface tidal velocity is about 2 knots (Fig. 10), and the residual drift velocity therefore about 0.4 knots. In Miramichi Bay and in the James estuary, where maximum tidal currents are less strong (¾ to 1 knot), the net velocity of the surface drift in the seaward direction is between 0.18 and 0.2 knots, and that of the bottom drift in the flood direction is between 0.1 and 0.2 knots. Drift velocities calculated from the mass transport of barnacle larvae (*Balanus improvisus*) are of this order of magnitude (.09 knots at 6.2 feet; .13 knots at 15 feet) (Bousfield, 1955, Table XIV).

SUMMARY

1. The present account describes certain physical features of the Miramichi estuary, New Brunswick, based on the results of investigations in 1950 and 1951, and on previous information.

2. Variations in the distribution of salinity, temperature and water transparency observed in 1951 are correlated with changes in precipitation, river discharge, wind velocity and other variables.

3. The principal features of the tidal circulation are described. Assuming complete mixing, the water exchange with the Gulf of St. Lawrence during a complete tidal cycle would be approximately 15%.

4. The residual or non-tidal circulation is described. Owing to the large and seasonably variable discharge of the Miramichi River, a net seaward drift, strongest on the south side of the estuary, of brackish water near the surface, and a landward counter-drift, strongest on the north side, of more saline water near the bottom is superimposed on the oscillating tidal currents. The boundary between the two opposing layers of drift, the level of no net motion, may be estimated to be approximately 10 feet in depth.

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Some Observations on the Movement of Pacific Salmon Fry through a Small Impounded Water Basin[1]

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ABSTRACT

A small-scale field experiment was conducted to investigate the migration of Pacific salmon fry through an impounded water basin, 2.4 acres in area. Pink, chum, coho, spring and sockeye fry were released at the upstream end. During nine days of operating a trap placed below the outlet dam, only pink and chum fry appeared. One-quarter of the total of these latter species moved through the impoundment and were recaptured. The migration of the fry was mainly confined to a period 1½ hours after sunset to 1½ hours before sunrise. The rate of migration of fry through the impoundment differed significantly from the movement of floats also released above the basin.

INTRODUCTION

On the Pacific coast of North America the damming of streams for power and irrigation presents an obstacle in the path of migrating salmon (*Oncorhynchus*). Various structures have been devised to allow adult salmon, moving upstream, to surmount some of these obstacles, but no satisfactory device insures safe downstream passage of their progeny. Certain difficulties are encountered in studying the migrating young fish. In general they cannot be seen without the aid of artificial light since some species and stages characteristically migrate at night. Those that move during the day are frequently obscured by turbid or wind-swept water. As a consequence most of the information relating to migratory behaviour has arisen from a limited number of field observations and laboratory studies. This information has produced conflicting outlooks. It is believed by some workers (Hoar, 1951; Clemens, 1951) that the physical force of moving water plays an important role in displacing free-swimming fry and smolts from fresh to salt water. Such a "drift" theory implies a passive migration, with young salmon oriented upstream, yet moving downstream by virtue of a lack of resistance to stream movement. Hoar (1953) recognizes that these fish are not completely at the mercy of moving water. "They are active fish and as they dart to and fro will move most easily and farthest with the current, and will at night go downstream rapidly until they can again see to maintain position with respect to fixed objects". On the other hand Pritchard (1943), when observing pink fry in McClinton Creek, recorded that "the fry are not passively carried by the current out to sea, but actually make a swift and vigorous migration".

With knowledge of the mechanics of fry migration both scant and inconsistent, the question of what the large impounded basins above dams would mean to young salmon is of major importance to conservation. If the migration is a

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passive one and dependent on the normal relations of uninterrupted streams, then the creation of quite unnatural water basins may form a formidable barrier to migration.

To investigate the problem, a small-scale field experiment has been conducted seeking to provide answers to the following questions:

1. Will salmon that normally migrate seaward in the fry stage (pink, *O. gorbuscha*, and chum, *O. keta*) move through impounded waters?

2. Do the other species of salmon in the fry stage (coho, *O. kisutch*, spring, *O. tshawytscha*, and sockeye, *O. nerka*) exhibit behaviour relations distinct from pink or chum under similar field conditions?

3. Are these fish merely subject to drift currents or do they actively move towards an outlet?

MATERIALS AND METHODS

The site chosen for the experiment was an impounded basin,[2] 2.4 acres in area and fed by a small stream (4.06 cu. ft. per sec.) diverted from the Nanaimo River (Fig 1). The basin and stream had been excavated to provide a source of water for a well supplying a nearby pulp-mill. Twenty-eight uniformly distributed

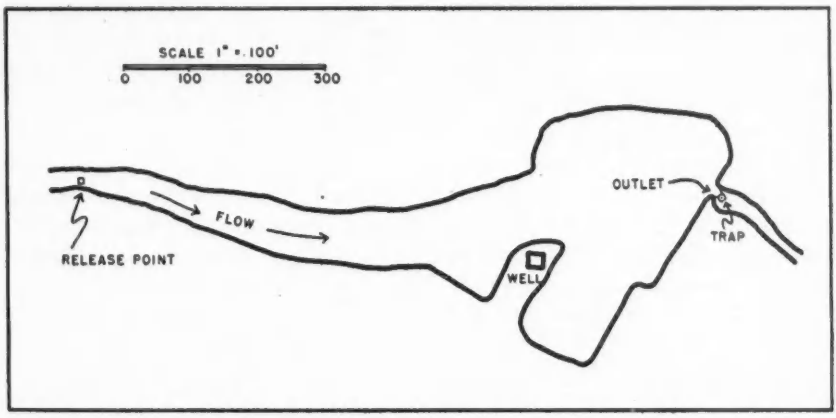

FIGURE 1. Map of impounded water basin, showing fry release point and recapture trap.

soundings all at least 20 feet from shore showed the depth of the basin to range from 4 ft. 2 in. to 6 ft. 0 in. with a mean depth of 4 ft. 11 in. The surface velocity at the upstream end (fry release point) was 0.5 ft. per sec. This decreased to 0.1 ft. per sec. at a distance of 150 feet downstream and was further reduced to approximately 0.003 ft. per sec. at the centre of the basin. A fish trap installed at the overflow ramp of the outlet provided a means of counting and examining all fish leaving the basin (Fig. 2).

[2]Recharge basin No. 41 Harmac Pulp Division, McMillan and Bloedel Co. Ltd., Nanaimo, B.C.

FIGURE 2. A view of the water basin, outlet dam and recapture trap.

The procedure was to liberate fry of the five species of Pacific salmon along with floats at a point upstream from the basin. Releases were made in the late evening, between 8:30 p.m. and 10:30 p.m. The effect of wind on the floats was obviated by suspending plastic "current vanes" at two depths (one half at 6 inches and the other half at 12 inches) from the barely surfacing corks. By periodically checking the trap the times of arrival of fish and floats were recorded.

The different species were obtained at an early stage of egg development from three localities—sockeye from Issaquah hatchery, Washington; spring salmon from Dungeness hatchery, Washington; chum, pink and coho from Nile Creek, Vancouver Island. They were cultured to free-swimming fry at the Nile Creek field station. Every attempt was made to expose them to identical environmental conditions during development. Light intensity, temperature, water flow and feeding were controlled in such a manner that the five species had very similar hatchery histories. Their ages differed slightly but none were more than three months past the time of hatching. Mean fork lengths were as follows: chum—39.5 mm., pink—34.5 mm., sockeye—33.3 mm., spring—44.1 mm., coho—40.6 mm.

Since the stocks of cultured fish were limited it was decided that only one multiple release would be made using the total of all five species. Preliminary experiments were therefore carried out with "wild" pink fry from the traps of the Nile Creek station. These experiments indicated that from 2 to 21 per cent of the

pink fry released into the stream a short distance above the basin would migrate through the impoundment and over the dam. However a profuse algal growth in the basin stranded the floats and plugged the screening of the trap to such an extent that accurate appraisal of the results was difficult. Consequently before the major experiment began the algae were removed by dragging a pipe frame along the bottom of the basin which freed the algal mass.

The major experiment commenced at 8:30 p.m. (P.S.T.) May 12, 1952. Four hundred sockeye and 600 each of spring, coho, chum and pink fry were released along with 50 floats.

The traps were examined at half-hour intervals during the night and hourly intervals during the day for two days. These were followed by morning and evening inspections on the third day and morning inspections only on the following four days.

As a check on the results an additional group of "wild" pink and chum fry were released immediately following the termination of the major test.

Because the basin had to be drained for cleaning, no further experiments were possible.

RESULTS

The trap counts (Table I) showed that 30.8 per cent of the pink fry and 14.4 per cent of the chum fry moved through the impoundment. This migration was confined almost entirely to the first three days after release. Sockeye, springs and cohoes did not move through the basin during the time of experiments.

The first pink and the first chum arrived at the outlet simultaneously 1½ hours after release, whereas the first float took 10 hours 55 minutes to drift the same distance. The modes of arrival times occurred at 4 hours after release for the fish, and 13 hours for the floats. It is seen (Fig. 3) that this is almost completely a night-time migration, beginning shortly after dark (10:30 p.m.) and ending rather abruptly towards dawn (4:30 a.m.).

Subsequent to the release of the cultured fish, 300 pink fry and 200 chum fry, which were trapped during their downstream migration in Nile Creek, were

TABLE I. Number of cultured pink and chum salmon fry recaptured at trap each day from the May 12 liberation.

Date: night of	Pink		Chum		Total	
	no.	%	*no.*	%	*no.*	%
May 12–13	86	14.3	60	10.0	146	12.2
13–14	80	13.3	19	3.2	99	8.3
14–15	19	3.2	2	0.3	21	1.8
15–16	0	0.0	0	0.0	0	0.0
16–17	0	0.0	0	0.0	0	0.0
17–18	0	0.0	1	0.2	1	0.1
18–19	0	0.0	4	0.7	4	0.3
Total	185	30.8	86	14.4	271	22.7

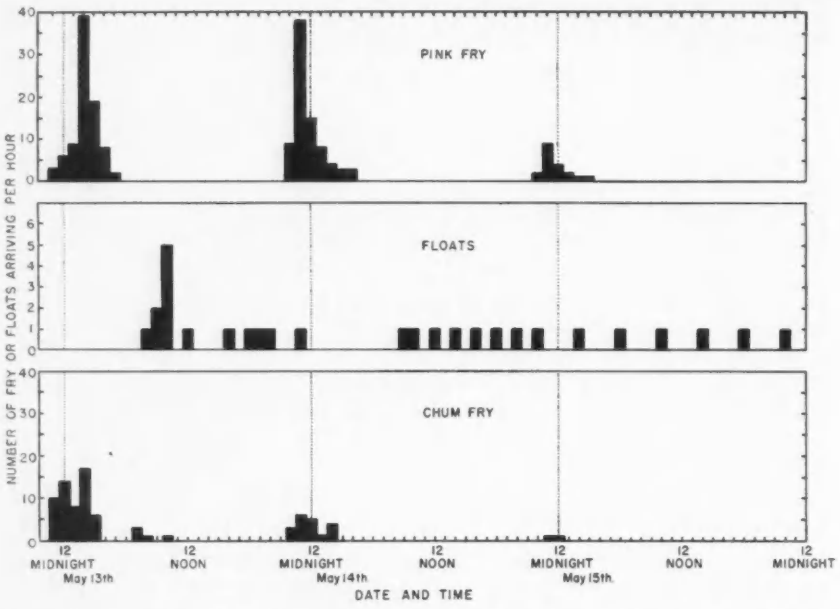

FIGURE 3. Rate of arrival of fry and floats per hour at the recapture trap. Releases made at upstream end of impoundment at 8:30 p.m., May 12.

released at 8:30 p.m., May 19. The trap was checked the following morning and again on the morning of the next day. Although a smaller fraction of the total number migrated (Table II) the timing pattern was similar to that of the major experiment.

Examination of a 33% sample of the stomachs of 126 yearling coho and trout caught in the trap during the week of the major experiment showed only one salmon fry (chum). The main contents were insects.

TABLE II. Number of wild pink and chum salmon fry recaptured at trap for two days following liberation on May 19.

Date: night of	Pink		Chum		Total	
	no.	*%*	*no.*	*%*	*no.*	*%*
May 19–20	32	10.7	11	5.5	43	8.6
20–21	18	6.0	2	1.0	20	4.0
Total	50	16.7	13	6.5	63	12.6

DISCUSSION

The salient feature of this study was that a considerable proportion of the two species of salmon at the normal migratory stage of their life history moved

through the area of quiet water, and at a speed exceeding drift currents. If the drift theory applied, the modal time of arrival of the fish would have been the same as that of the floats, instead of only one-third as long.

It is evident that a fundamental difference exists between the passive movement of floats and active swimming of fry. The passage of floats would be a function of the barely perceptible flow of water through the impoundment. Spatial movement of floats would be confined to one plane and in the general direction of the outlet. Fry are capable of moving through all directions, limited only by the surface and bottom. If a mean swimming rate is assumed as well as a random movement, fry should arrive at the outlet within the same modal time period, with respect to the movement of the floats. Since they arrived earlier than the floats, some bias must be operating to produce a net movement in the direction of the outlet. Fry must therefore be swimming during darkness at a greater rate than the current drift in a direction predominantly toward the outlet. It would appear that random movement enhanced by passive drifting does not satisfy the characteristics of migration through the impoundment. If fry are able to detect currents of very low velocity they would of necessity have to swim at a greater rate than that of the current to appear at the outlet in the interval described, indicating an independence from passive movement in slow-flowing water.

The fact that approximately three-quarters of the total number of pinks and chums released were not recaptured during the nine-day period is difficult to explain. Stomach analysis of coho and trout juveniles showed that excessive predation was unlikely. There was little if any chance that they escaped through the trapping system. It is possible, however, that the fraction that did migrate were the only members of the group that were at the critical level of metabolic stress found to characterize young salmon in fresh water (Hoar and Bell, 1950). The others, in this case, would presumably remain in the area until further development brought them to a similar critical level. Evidence against this interpretation lies in the fact that a large percentage of the second group of fish released also failed to migrate. These latter fry had been captured during their downstream migration and consequently were considered to be "migratory fish". It is possible that in faster water more of these fish would have travelled the same distance during the time of the experiment. For this reason it is difficult to interpret the effect of the impoundment on the migration of young fish. The evidence that some fish moved through points out that the impounded water was not a total block, while the fact that others did not suggests that it may be a a partial block.

The periodic checking of the trap provided the times of migratory activity of these fish. While the exact times of commencement and termination of migratory activity in the basin cannot be determined, the first fish of the night were found in the trap by approximately 1½ hours after sunset while the last (except for one or two fish) arrived approximately 1½ hours before sunrise. The time of migratory activity of the fry appears then to be closely associated with fluctuations in light intensity. This presents an interesting contrast to upstream

migrating adult coho and spring salmon observed at Stamp Falls, Vancouver Island, where migratory activity increased rapidly at sunrise and decreased at sunset (MacKinnon and Brett, 1953).

SUMMARY

Fry of the five species of Pacific salmon were released at the upstream end of a small impounded water basin. Their migration through the basin and the rate of movement of floats, synchronously released, were checked at a trap placed below the outlet dam.

Approximately one-quarter of the pink and chum fry moved through the impoundment and were recaptured during a nine-day recovery period.

Other salmon fry did not leave the basin during the period of operation.

The movement of pink and chum fry was significantly different from that of small floats. The first fry arrived at the outlet one hour 25 minutes after liberation; the first float took 10 hours 55 minutes.

The migrating fry passed over the dam only during the night, mainly from 1½ hours after sunset to 1½ hours before sunrise.

ACKNOWLEDGMENTS

Appreciation is extended to Mr. R. E. Simkins, Superintendent, Harmac Pulp Mill, for permission to use the site as an experimental area, and to Mr. A. R. Woodhouse for his co-operation during the course of the experiment. Special note is made of the effort put forth by Messrs. W. Caulfield and H. Neate of the Nile Creek field station. Their assistance in culturing the fish and constructing the trap was greatly appreciated.

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Notes on the Seaward Migration of Pink and Chum Salmon Fry[1]

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ABSTRACT

The seaward migration of pink and chum salmon fry takes place at night. Strong light is avoided. In pink salmon negative rheotaxis (swimming with a current) is strongly developed and migration is not primarily effected by random swimming and passive displacement. Downstream movement is mainly at or close to the surface. In slack water vertical distribution is more uniform. In the shortest streams examined, each night's migrants appeared to reach the sea before daybreak. In a longer stream, fry were seen to bury themselves at the onset of daylight. After being held in fresh water for an undetermined period, fry show positive rheotaxis and schooling behaviour and no longer avoid light. Behaviour of fry after reaching the sea also differs from that shown during actual migration. Changes in behaviour may coincide with commencement of feeding.

INTRODUCTION

Recent studies by Hoar (1951, 1953) and MacKinnon and Hoar (1953) have provided much information on the behaviour of pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) fry. These authors have shown that under the conditions of their experiments the fry are active both day and night; that they tend to move into currents; that in daylight they show positive rheotaxis and aggregate into schools; that they seek the light.

These findings have led to the conclusion that the downstream migration of these species is largely a process of "displacement".

> Chum fry prefer relatively bright light and move into strong currents by day. As the light intensity falls, rheotactic responses, which are to a large degree dependent on vision, fail, and these fish pass downstream in shoals. The fact that such mass movements occur during a rather precise period of the night is probably due to the dark adaptation of the eye and a period of night blindness. . . . They are active fish and as they dart to and fro will move most easily and farthest with the current and will, at night, go downstream rapidly until they can again see to maintain position with respect to fixed objects.
>
> Pink salmon fry have not been intensively studied but general comparisons indicate that their behaviour is similar to that of chums [Hoar, 1953].

Again,

> their [chum and pink] behaviour is such that, during the night, downstream displacement is inevitable. It is emphasized that juvenile seaward-moving salmon are active and vigorous, but, at the same time, carried seaward by the currents.

While the experimental findings on which this view is based are not in question, field observations seem to show that the responses of migrating fry are commonly quite different from those described above. The following notes,

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except where otherwise indicated, refer to pink salmon but there is at present no evidence to suggest that chum salmon behaviour is essentially different.

DIURNAL PERIODICITY OF MIGRATION

The operation of counting weirs at McClinton Creek (Queen Charlotte Islands), Morrison and Nile Creeks (Vancouver Island) and Hooknose Creek (King Island) has demonstrated that in these localities downstream migration of pinks and chums occurs almost entirely during hours of darkness. Often the daylight catch is nil, even at periods when many thousands of fish are trapped each night. Occasionally, under conditions of flood or high turbidity, small numbers of fish pass downstream during the daytime. Daytime observations fail to substantiate the view that the fish are at this time in bright light or that they are resisting displacement by swimming against the current. Commonly, few or

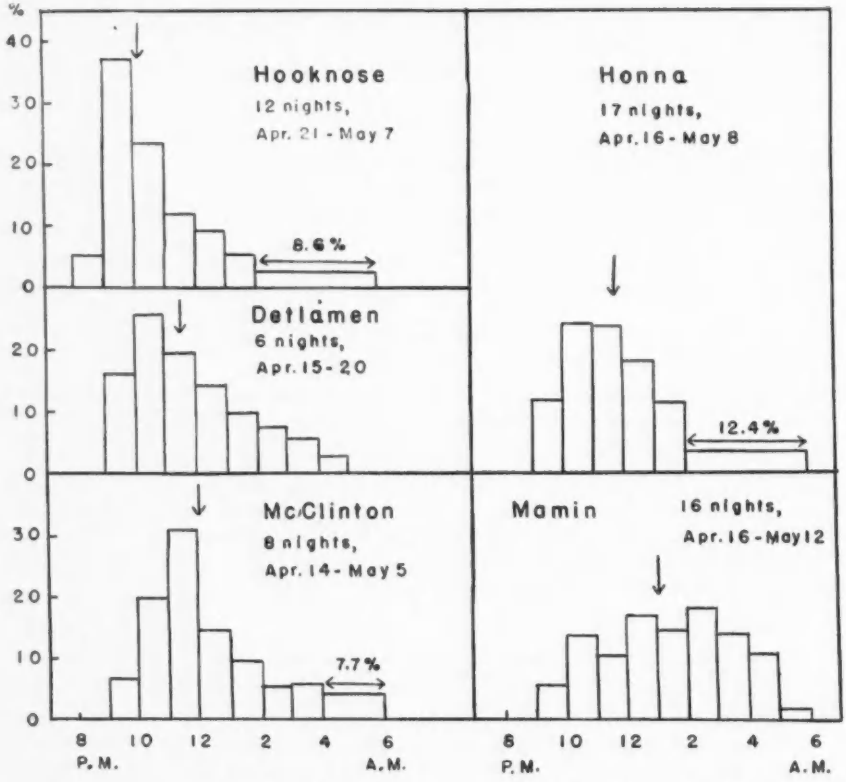

FIGURE 1. Percentage of pink salmon fry caught, by hours, during nightly migration. Catches made on various nights have been summed. Arrows represent mean time at which 50% of the run was completed.

no fish can be seen between dawn and dark. Sometimes individuals or small parties of fry can be found, stemming the current in the manner envisaged by the displacement theory. These fish are far too few to make a significant numerical contribution to the nightly migrations recorded in these localities. The apparent scarcity of swimming fish during the day cannot be attributed to difficulty of observation, since the use of a flashlight at night often discloses large numbers. The absence of visible pink salmon fry during daylight hours was noted by Pritchard (1944) who stated that the fish were hiding under stones and roots.

Although Pritchard (1944) considered that the rate of migration throughout the hours of darkness in McClinton Creek was generally constant, recent observations on this and other streams have given a different result. The passage of migrants at a given spot often shows a definite peak and the greater part of the nightly catch is frequently made during a 2- or 3-hour period of the approximately 7 to 8 hours of absence of daylight. "Absence of daylight", as determined by subjective impressions, necessity of using lanterns to locate and examine nets, etc., was considered to last from about 8.30 p.m. to 5.00 a.m. at the beginning of the season of observations and from 9.00 p.m. to 4.00 a.m. in the closing stages of the operations (all times Pacific Standard).

Figure 1 shows the percentage of the total nightly catch recorded during consecutive hours in five streams which were investigated in April and May, 1953. Observations were made on Hooknose Creek by J. I. Manzer, on the Mamin River by W. P. Wickett, on the Honna River by J. G. Hunter, on McClinton Creek by E. A. R. Ball and on Detlamen Creek by F. Neave. Except for Hooknose Creek, all these streams are situated on Graham Island.

In each case a fyke net with a rectangular aperture of 1 ft. by 2 ft. was used, the accumulated fish being removed at the end of each hour during the indicated nightly periods (in some instances, as shown in the figure, the tail-end of the run was allowed to accumulate for more than one hour).

In all these streams the migration, as measured at a point near the stream mouth, began at about the same time in the evening. However, the halfway point in the night's catch was not reached at the same time in all cases. The pattern of the nightly run is discussed further below.

ACTION OF FRY IN RELATION TO CURRENT

Pritchard (1944) states that "the fry are not passively carried by the current out to sea, but actually make a swift and vigorous migration. They may move downstream as quickly as 15 to 20 ft. (4.6 to 6.1 m.) per sec."

Such movements were readily observed in Detlamen Creek (April 1953) on smooth water surfaces on nights when pink salmon fry were migrating in numbers, although the actual speed of the fish was not measured. Many of the fish travelled right at the surface and created a "bow-wave" which could be seen under conditions of minimum illumination. The judicious use of artificial light confirmed the identity and movements of the migrants. The fish travelled singly, at a speed much greater than the current, and often appeared to avoid expertly the solid objects which sometimes made a straight course impossible. While

these observations are insufficient to prove that all or even most of the fry were travelling downstream in this manner, no random or upstream swimming was observed. On a night when downstream surface swimming was observed, nets set at a spot where the water was 18 inches deep showed that 62% of the catch was made in the top 6 inches.

Night observations indicated that on reaching slack water (tidal influence) the migrants swam slowly in a random manner and distributed themselves more uniformly from top to bottom.

Hoar (1953) reports the development of negative rheotaxis in chum salmon which had been held in captivity for several weeks. "Experiments indicate that a rising temperature will change a predominantly positive rheotaxis to a negative rheotaxis in which chums swim rapidly with the current—usually more rapidly than the current". However in Detlamen Creek the temperature was always relatively low and was observed to fall from 5.2°C. to 4.3°C. during a night on which much negative rheotaxis was seen.

RESPONSES TO LIGHT

In the streams to which reference has been made, swimming fry could not be found in any number until approximately 2 hours after sundown. Presumably they avoid light at this stage. Even if it is assumed that emergence from the gravel and migration to the sea are completed in one night, the deferring of emergence until dark seems to imply an awareness of light conditions and a negative phototaxis. The view that the newly emerged fry avoid light was supported by observations made while the nightly migration was in progress (Detlamen Creek, April 1953). When a portion of the stream was illuminated by artificial light, fry travelling at speed downstream frequently passed through the fringe of the illuminated area without stopping. Those whose course took them into a broad area of bright illumination swung around with head upstream, sank to the bottom and frequently pushed their way under pebbles. Fry captured during their migration often crowded into the least illuminated angle at the bottom of a pail.

Although, as indicated in Figure 1, the nightly migration in most of the streams investigated was virtually completed well before daylight, in the Mamin River considerable numbers of fry on some occasions continued to travel downstream until daybreak. At this time (varying from about 5.00 a.m. to 4.00 a.m. with the advancing season) net catches fell off sharply to near zero and fry could no longer be seen in the river. Wickett was able to observe fry burying themselves in the stream bottom and thus reacting to the onset of daylight in the same way as the Detlamen Creek fry behaved when exposed to artificial light.

DISCUSSION

Field observations seem to show clearly that at the time of their downstream migration pink salmon fry commonly (1) show strong negative rheotaxis, (2) avoid light, (3) do not exhibit schooling behaviour by day or night.

The effect of this behaviour is the evacuation of a stream in the shortest

possible time, under cover of darkness. The survival advantages of this procedure can hardly be doubted in view of the vulnerability of these fry to predation while in fresh water.

The data suggest that most fry do not swim actively until the night on which they start their migration and that emergence into the stream tends to take place during the first half of the night. In Hooknose Creek, where spawning is mainly confined within a distance of one mile from the trapping point, 50% of the nightly catch was made on average by about 10.15 p.m. and over 90% of the run had passed by 2.00 a.m. In Detlamen and McClinton Creeks and the Honna River, where spawning grounds extend for 2 to 4 miles and the average distance covered by the fry is therefore greater, the main part of the run tended to be somewhat later and in the Mamin River, with 8 to 10 miles of productive stream above the trap, fish frequently ran in numbers until dawn.

These migration patterns do not seem to fit the suggestion that the migration is largely confined to a period of "night blindness", since the latter condition might be expected to occur at about the same time in most of these streams.

Rheotaxis, i.e. orientation with respect to current, is usually regarded as dependent on vision. The downstream night migration of pink salmon fry frequently takes place under such dark conditions that some other form of directional control can be suspected. It seems not impossible that, in a natural stream, sensitivity to turbulence or to varying water pressures created by banks, bottom or other physical obstacles may take the place of optical stimulation. However, the observations recorded in the present account do not permit a ciritical examination of the problem.

The fact that in most of the localities investigated the run tapered off well before dawn seems to indicate that in the shorter coastal streams the migration from spawning ground to ocean is commonly completed in a single night. The Mamin River observations suggest that fry which have not completed their journey during the first night may hide during the ensuing day and then resume their migration. There are at present no direct data to show whether this behaviour continues to prevail in the case of fish whose journeys in long river systems must extend over many days (or nights). However, it may be pointed out that the behaviour exhibited (migrating at night, hiding during daylight), while advantageous for the avoidance of enemies, makes no provision for feeding. Fry captured during migration and held in pens soon exhibit schooling behaviour and positive rheotaxis and do not seem to avoid light. Fry which have reached the ocean under natural conditions can also be observed swimming in schools in bright light, in contrast to their recondite habit in the streams.

It is suggested that this change in behaviour is associated with the developing necessity for seeking food, whether or not the migration has been completed in the meantime.

It would seem that the responses recorded by Hoar and MacKinnon are characteristic of fry at a period *after* migration would normally have been completed or at least initiated, and after striking changes in behaviour have taken place.

The small numbers of fry which are sometimes seen in short streams, exhibit-

ing schooling behaviour and positive rheotaxis in daylight, have presumably failed to make their exit in the usual manner and are behaving like fry held in captivity. Their eventual evacuation, as well as the later stages of migration in long rivers, may not improbably be accomplished by a "displacement" mechanism.

Finally, it must be concluded that the use of "marked" fish for demonstrating the speed of migration and the attendant mortality is open to criticism in cases where the fry have been held for a period and especially when they have not been given an opportunity to avoid exposure to light.

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Change in Bottom Temperatures on the Scotian Shelf[1]

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ABSTRACT

A comparison of recent bottom temperatures on the Scotian Shelf with those observed in the period 1934 to 1939 shows that, in general, these temperatures have been higher by from one to three Centigrade degrees in the more recent period. The change has been due to the variation in the intermediate layer which was both colder and of greater thickness during the early period.

INTRODUCTION

McLellan (1954) has discussed bottom temperatures on the Scotian Shelf as observed by the Atlantic Oceanographic Group since 1950, making certain generalizations concerning the temperature regime on various portions of the Shelf as a function of location and depth. In order to understand the distribution of bottom temperatures on the Shelf, it is necessary to consider the stratification into three distinct layers (which Hachey, 1942, has shown to typify the area) and the seasonal variations which take place in the upper and intermediate layers. In the deep Scotian Gulf (Hachey, 1937) the bottom waters are subject to non-systematic replacement through incursions of slope water (Hachey, 1953; McLellan, Lauzier and Bailey, 1953).

The series of extensive seasonal cruises, during which the reported temperatures (McLellan, 1954) were observed, was initiated in 1950. It represents a continuation of the long term study of the waters on the Scotian Shelf which was begun by the Fisheries Research Board of Canada some 17 years previously. In the years 1934 to 1939, 19 surveys were made over the network of stations described by Hachey (1942, fig. 1). Various features of the waters on the Scotian Shelf have been discussed from the results of these surveys, furnishing much of the background for our present understanding of these waters.

It is of interest, then, to make a comparison of bottom temperatures as observed over the two periods to ascertain if there has been any significant change in this biologically significant parameter. In particular, one may wish to speculate as to how the general trend towards higher temperature which has been displayed by surface waters (Lauzier, 1952) is reflected in bottom conditions over the Shelf.

METHOD

Hachey (1942) plotted the distribution of bottom temperatures for each of three seasons in 1938. Because of the differences in scale, however, these plotted data are not readily compared to the later data as presented by McLellan (1954).

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For this reason, bottom temperatures from a number of early surveys have been plotted on charts of the same scale as those used for the later data. No reference has been made to earlier plots, so that the contouring would be biased only by the same conceptions that influenced the plotting of the 1950–53 data. Considerably more latitude has been allowed in interpreting the results than was shown in Hachey's (1942) plots. In particular, departure from strict contouring procedures has been made to conform with the idea that bottom temperature in the central area of the Scotian Shelf is very largely a function of depth. This is especially noticeable over LaHave and Sambro Banks where these banks appear as regions of depressed bottom temperatures surrounded by areas of higher temperature.

Differences Inherent in Survey Networks

In any oceanographic survey, it is inevitable that the results will be biased to a certain degree by the design of the survey network and by the methods and instruments used in the observations. For this reason, the network of observations is usually indicated in any discussion of results, and must be kept in mind when the results are interpreted. In the presentation of bottom temperatures from recent surveys, the lines along which observations were made have been shown by light dashed lines on the plotted diagrams. These indicate where bathythermograph lowerings have been made to bottom with a spacing of approximately ten miles between observations. On the plots of data from earlier surveys, the locations of the individual hydrographic stations have been shown. In the early surveys, temperatures were never recorded at the very bottom but only as close to the bottom as was consistent with the safety of equipment (in very few cases do the records show a difference between sounding and deepest sampling depth which is as great as five metres). How closely the deepest observations approximate to actual bottom temperatures depends upon the intensity of vertical temperature gradients which may have existed near the bottom.

The geographic distribution of observations differed significantly for the two periods. The early surveys contained no observations east of Canso Bank nor west of the line over Roseway and LaHave Banks. In addition, the size of vessel available for survey purposes restricted the offshore range, so that the outer portions of the Shelf were not covered. In one particular region (the shallow water of Sambro Bank), the earlier surveys provided detail missing in the later series. Sambro Bank is sufficiently elevated so that its shallower parts are, at times, wholly within the intermediate layer, and so show bottom temperatures lower than the surrounding deeper area. No comparable observations have been made in surveys since 1950, as no line of observations crosses Sambro Bank.

OBSERVATIONS

The two years which have been selected for comparison are 1938 and 1952, observations being available from each year for the winter, spring and summer seasons. The bottom temperatures observed during these surveys are shown in Figures 1 to 6. To illustrate the variations from year to year within the earlier period, results are also shown for the winter of 1937, the spring of 1935, and the summers of 1934 and 1936. These follow in Figures 7 to 10 inclusive.

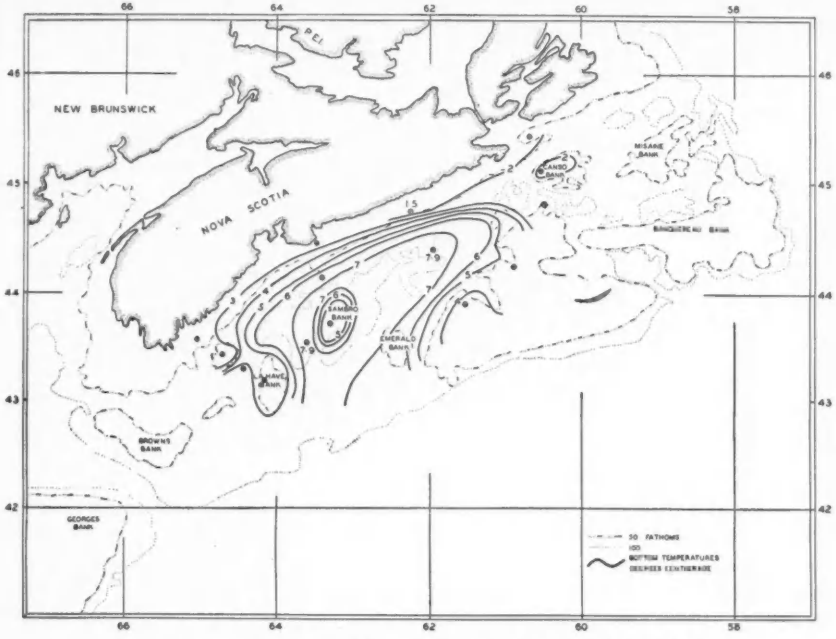

FIGURE 1. Bottom temperatures observed from January 24 to 29, 1938.

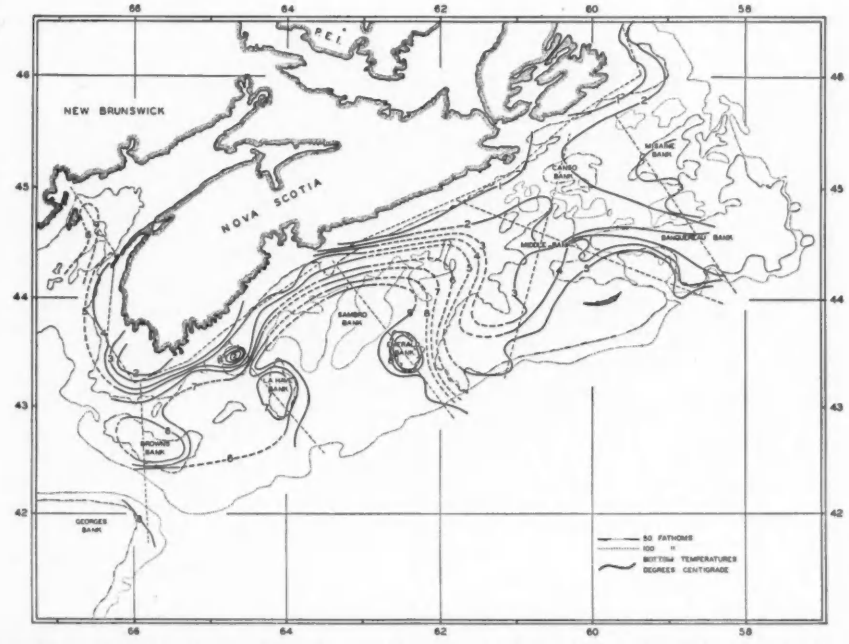

FIGURE 2. Bottom temperatures observed during cruise S-4, February 15 to March 18, 1952.

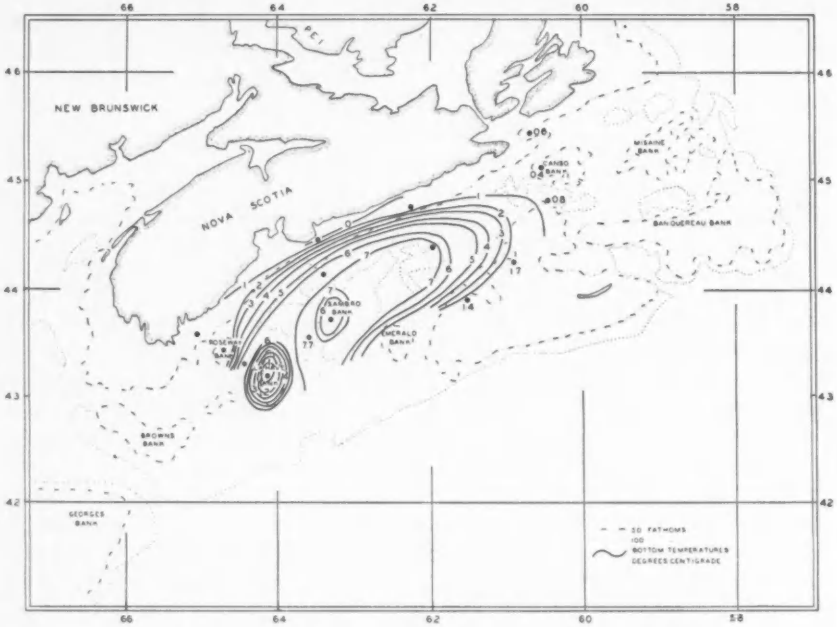

FIGURE 3. Bottom temperatures observed from April 26 to May 3, 1938.

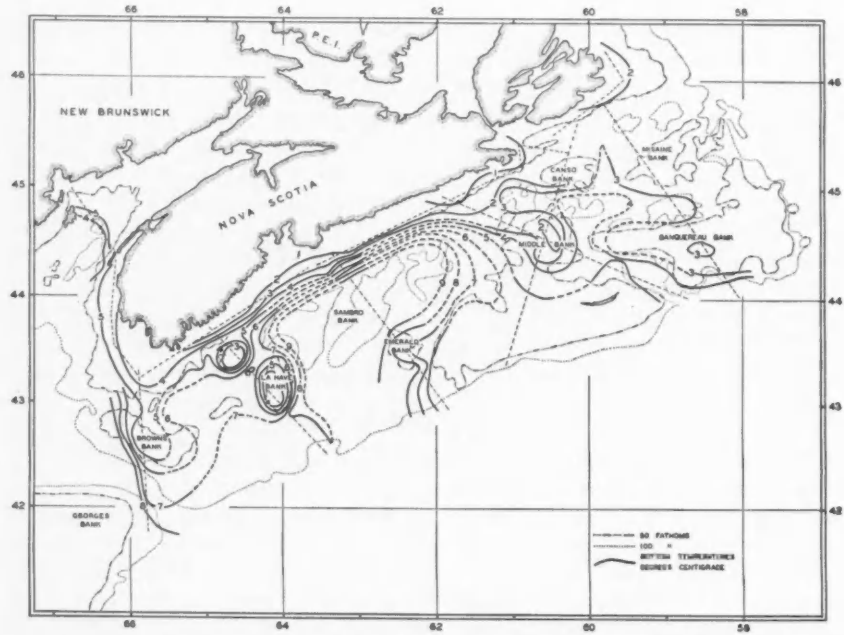

FIGURE 4. Bottom temperatures observed during cruise S-7, April 29 to May 11, 1952.

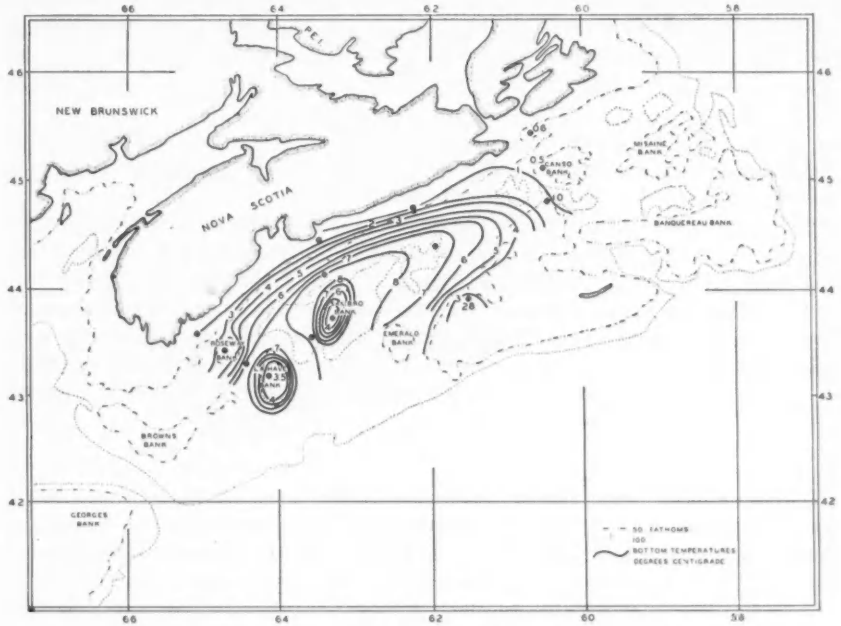

FIGURE 5. Bottom temperatures observed from August 26 to September 3, 1938.

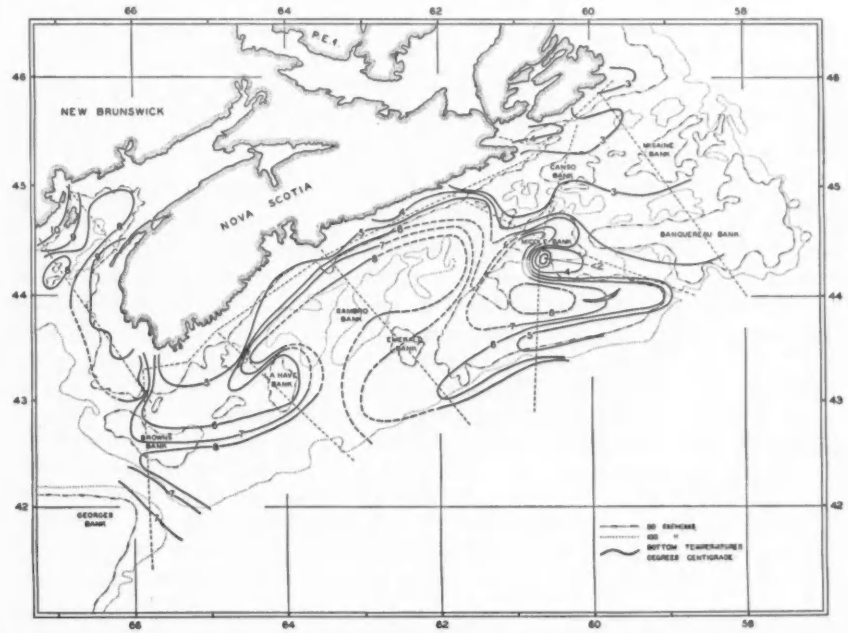

FIGURE 6. Bottom temperatures observed during cruise S-10, August 14 to September 5, 1952.

(*a*) WINTER 1938 AND 1952

Bottom temperatures as observed between January 24 and 29, 1938, are plotted in Figure 1, and may be compared with those in Figure 2, representing observations between February 15 and March 18, 1952.

The 1938 observations, having been made somewhat earlier in the year, may represent conditions before winter chilling has had its maximum effect. The following points of comparison may be noted.

1. The detail around Sambro Bank, as discussed above, is not comparable.
2. Temperatures on Sable Island and Canso Banks were closely similar, while the inshore temperatures were slightly higher in 1938 than in 1952.
3. The highest temperatures observed in the deep water of the Scotian Gulf during the 1938 cruise were 7.9°C., whereas temperatures higher than 9°C. were found in 1952.
4. In 1938 temperatures on LaHave Bank were lower than 5°C., while in 1952 they were but slightly under 7°C.

(*b*) SPRING 1938 AND 1952

Figure 3 shows the plotted distribution of bottom temperatures from observations between April 26 and May 3, 1938, which may similarly be compared to results from April 29 to May 11, 1952, as shown in Figure 4. Points of comparison are:

1. LaHave Bank had temperatures three Centigrade degrees lower in 1938 than in 1952, while the bottom water on Roseway Bank was approximately one degree colder in 1938.
2. The waters on Canso Bank and in the inshore area were somewhat cooler in 1938, being as low as 0.4°C. where, in 1952, temperatures were between 1°C. and 2°C.
3. Deep water in the Scotian Gulf was somewhat warmer in 1952, being over 9°C. as compared to a maximum of 7.7°C. in 1938.

(*c*) SUMMER 1938 AND 1952

Summer conditions in 1938 are represented in Figure 5, which portrays bottom temperatures from the survey of August 26 to September 3, and compares with the results from August 14 to September 5, 1952 (Fig. 6) in the following respects:

1. Temperatures in the Scotian Gulf were slightly over 8°C. in both cases, representing a lowering with the progress of the year in 1952 and a rise in 1938.
2. The eastern sector and the inshore areas were from 2°C. to 3°C. colder in 1938 than in 1952, as was Sable Island Bank.
3. The bottom temperature observed on LaHave Bank in 1938 was 3.5°C., whereas temperatures there were between 5°C. and 6°C. in 1952.

(*d*) WINTER 1937

Winter bottom temperatures for 1937 are plotted in Figure 7. The survey represented by this figure was carried out during the period February 4 to 10, and for this reason would be expected to show slightly more of the effect of

winter chilling than did the winter cruises of 1938 (Fig. 1). A comparison of the two indicates that bottom temperatures were slightly lower in 1937. Canso and Sable Island Banks showed temperatures about one Centigrade degree lower than in 1938. The maximum observed in the deep Scotian Gulf was 6.9°C. as compared to 7.9°C. in 1938. The bottom temperature observed at the station on LaHave Bank was 3.2°C., more than a degree lower than in 1938.

(*e*) SPRING 1935

Bottom temperatures in the spring of 1935 are represented by Figure 8, which shows the results from a survey in the period May 14 to 21. Temperatures in the shallow eastern sector, and along the coast, were approximately one degree lower than in the spring of 1938 (Fig. 3), and deep water temperatures in the Scotian Gulf were approximately one degree higher. In the western sector conditions were closely similar in the two years.

(*f*) SUMMER 1934

The bottom temperatures for this season (Fig. 9) have been shown because they represent conditions at a time (August 8 to 22, 1934), when the deep bottom layer had an increased effect on temperatures over the Shelf. Although maximum temperatures were only slighter higher than in the summer of 1938, the thickness of the bottom layer produced a temperature of 7.3°C. at the Sambro Bank station, some four degrees higher than in 1938.

(*g*) SUMMER 1936

Bottom temperature distribution from the survey of August 22 to 27, 1936 (Fig. 10), shows a minimum effect of the warm bottom layer. The maximum temperature observed in the Scotian Gulf was 6.9°C., over a degree lower than in either 1938 or 1934. These low temperatures in the bottom layer were accompanied by temperatures on LaHave Bank and Sambro Bank which were lower than 3°C. and 4°C., respectively.

DISCUSSION

In general, it would appear that bottom temperatures on the Scotian Shelf in the period 1934 to 1939 tended to be somewhat lower than those observed since 1950. The implications of this are different for the different subdivisions of the area.

(*a*) SCOTIAN GULF

This deep water seems to be subject to marked non-seasonal changes which are probably related to periods when the bottom layer is renewed, or partly renewed, through incursions of slope water. For this reason, one should not assume that, because three of the 1934–39 surveys found colder deep water than any of the 1950–53 surveys, these waters were consistently cooler at that time. On the other hand, it may point to an increase in the frequency of slope water incursions in recent years.

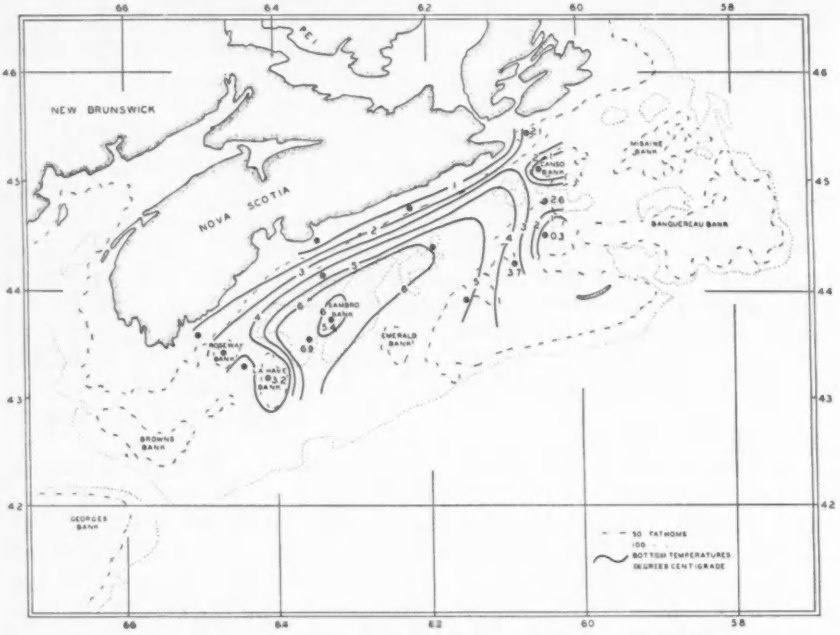

FIGURE 7. Bottom temperatures observed from February 4 to 10, 1937.

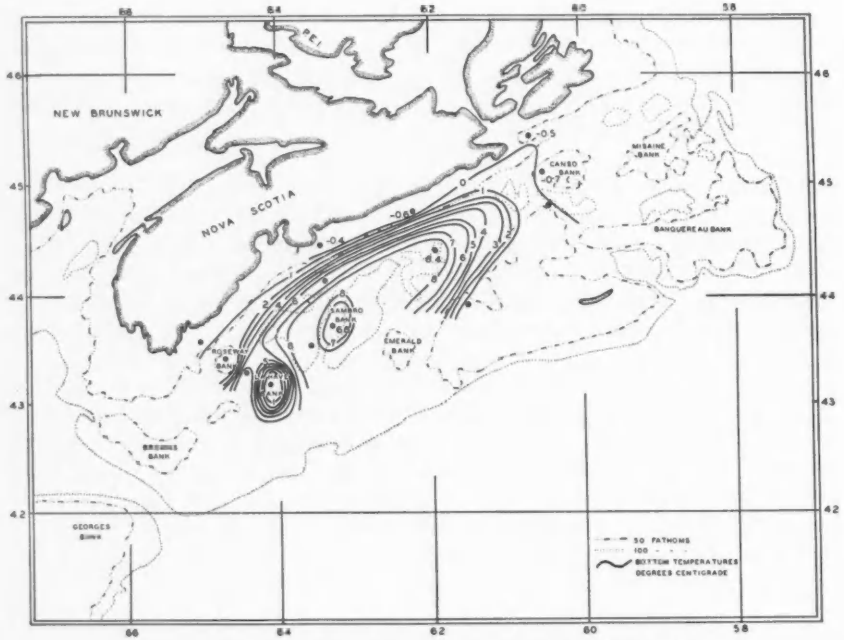

FIGURE 8. Bottom temperatures observed from May 14 to 21, 1935.

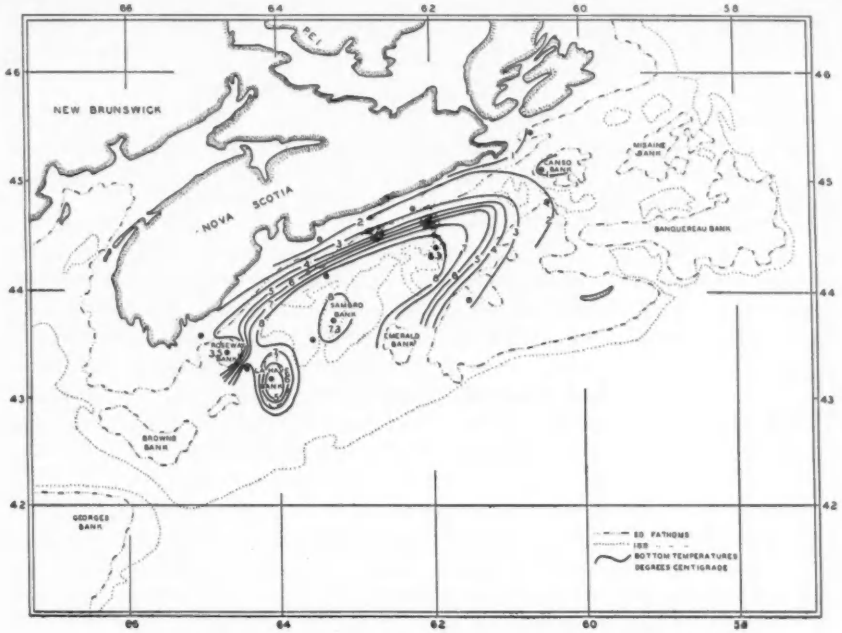

FIGURE 9. Bottom temperatures observed from August 8 to 22, 1934.

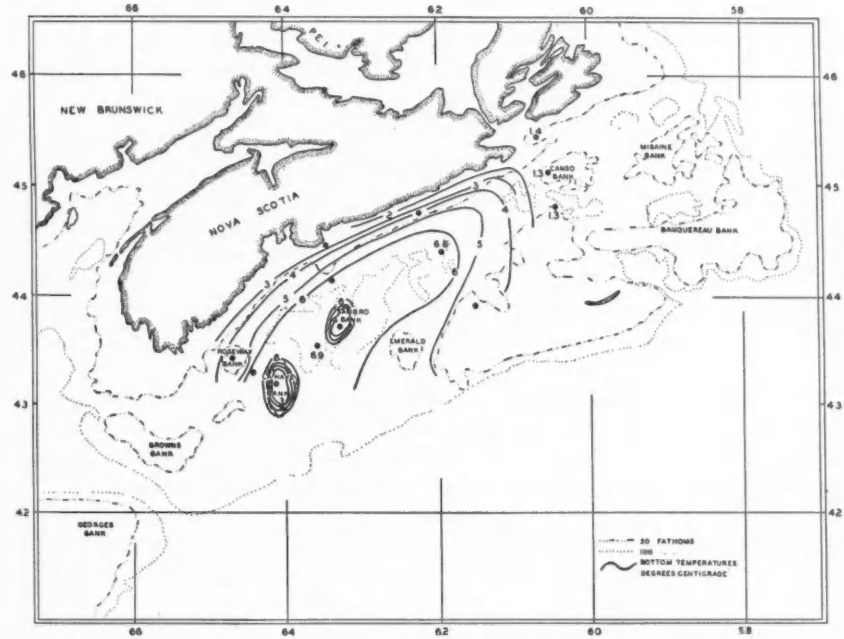

FIGURE 10. Bottom temperatures observed from August 22 to 27, 1936.

(*b*) EASTERN SECTOR

The area including Canso Bank, Sable Island Bank and the eastern shore of Nova Scotia during the 1934–39 period consistently displayed temperatures which were from one to three degrees lower than those observed since 1950. As these areas represent bottoms which are normally within the intermediate layer, one would suspect that this layer may have been warmer in the recent years than during the early period.

(*c*) LAHAVE BANK

Bottom temperatures on this Bank were consistently from two to three degrees lower in the period 1934–39 than in the later period. McLellan (1954) has classed this area as one which lies normally within the bottom layer and will show temperatures markedly lower than the deep waters of the Scotian Gulf only when the intermediate layer becomes thicker or deeper than usual. It would appear that during the 1934–39 period, this Bank lay normally within the intermediate layer, and a greater thickness of this intermediate layer is implied.

VARIATIONS IN THE INTERMEDIATE LAYER

During both periods of observations, a station has been regularly occupied between LaHave and Roseway Banks. Station 123 in the early surveys was located at Latitude 43°19′N., Longitude 64°25′W., and station 16 in the latter

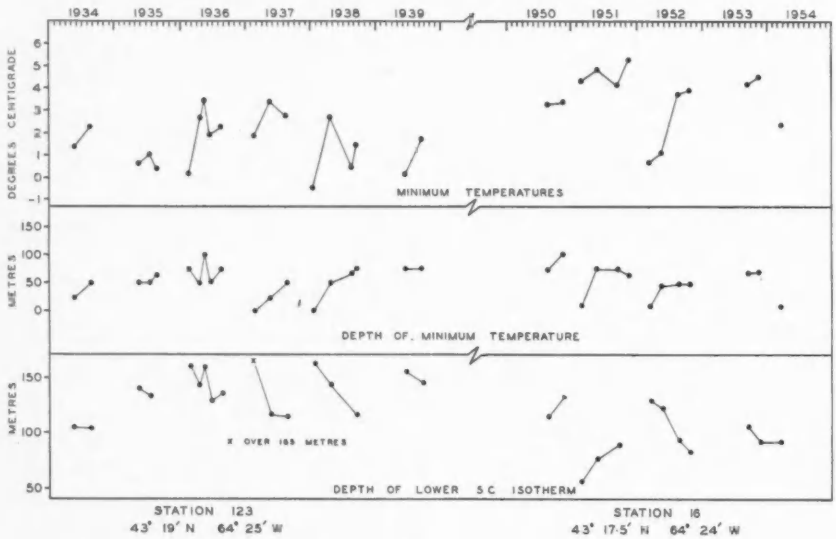

FIGURE 11. Variations in the intermediate layer between LaHave and Roseway Banks from 1934 to 1939 (station 123, Lat. 43°19′N., Long. 64°25′W.) and from 1950 to 1954 (station 16, Lat. 43°17.5′N., Long. 64°24′W.).

surveys at Latitude 43°17.5′N., Longitude 64°24′W. From a comparison of observations at these stations, changes in the intermediate layer may be detected.

In Figure 11, the minimum observed temperature, the depth at which the minimum occurred, and the depth of the lower 5°C. isotherm (which Hachey, 1942, has used to designate the lower limit of the intermediate layer), are plotted for every occupation of station 123 or station 16. It may be seen that:

1. The minimum temperature has been generally higher since 1950 than in the earlier period. Eight of the 13 surveys since 1950 found the minimum temperature higher than during any of the previous surveys. Only in March and May, 1952, were observed minima as low as the mean value for the minima in the 1934–39 period.

2. The depth at which the minimum temperature occurred varied little from one period to the other.

3. The depth of the lower 5°C. isotherm has been noticeably less in the period since 1950 than in the early period. An extreme case was observed in November, 1951, when there was no water at station 16 with temperature below 5°C. This decrease in thickness of the intermediate layer would explain the higher temperatures observed on LaHave Bank in recent years.

Hachey (1938) has shown the cold intermediate layer on the Scotian Shelf to be the result of transport from the northeast rather than winter chilling *in situ*. It would appear that this layer is continuous, at least during part of the year, with the similar feature in the Gulf of St. Lawrence which Lauzier (1952 unpublished) has shown to be formed, at least in part, by winter chilling *in situ*. The depth of the intermediate layer on the Scotian Shelf probably reflects the depth of the winter-chilled layer in the Gulf of St. Lawrence. The marked difference observed in this layer during the two periods of observations is due to a decrease in the intensity of winter cooling during the recent years.

SUMMARY

1. A comparison of recent bottom temperatures on the Scotian Shelf with those observed during an earlier series of surveys between 1934 and 1939, shows that, in general, bottom temperatures tend to be higher in the recent years.

2. In the shallow eastern sector, temperatures have been from one to three degrees higher in recent years than in the earlier period.

3. Higher temperatures have been observed in the deep Scotian Gulf within recent years, but there is reason to avoid a categorical statement regarding this area.

4. The bottom waters on LaHave Bank have shown temperatures which were consistently from two to three Centigrade degrees higher than those observed between 1934 and 1939.

5. The variation in bottom temperatures may be explained by the changes which have taken place in the intermediate water layer. This layer was noticeably colder and thicker in the early years than it has been since 1950, probably reflecting changes in the climate of eastern Canada.

ACKNOWLEDGMENT

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Resistance and Tolerance of Young Speckled Trout (*Salvelinus fontinalis*) to Oxygen Lack, with Special Reference to Low Oxygen Acclimation[1, 2]

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ABSTRACT

Samples of trout were exposed to flows of water containing constant low concentrations of oxygen (produced by equilibrating aerated water with nitrogen). At 9°–10°C. minimum tolerance levels were defined by determining the lowest oxygen level permitting survival of 5%, 50% and 95% of the fish for a period of 5,000 minutes. Median resistance times for samples of fish exposed to lethal levels of oxygen were also determined. Within their first year, most trout reared in aerated water could withstand oxygen concentrations down to 1.9 mg.O_2/l. The 50% tolerance level was 1.75 mg.O_2/l. Most fish died at 1.5 mg.O_2/l. Acclimation to low

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(but not lethal) oxygen levels occurred; for a drop of 1.0 mg.O_2/l. in environmental oxygen concentration, the tolerance level decreased by approximately 0.09 mg.O_2/l. and resistance times at given lethal levels increased up to five-fold. By acclimations trout could exist at 1.05 mg.O_2/l. without direct lethal effects occurring. Between 20 and 33 hours were required for the fish to acclimate to a change of 1.0 mg. per liter in the oxygen concentration of the environment. Acclimation to low levels of oxygen was accompanied by an apparent increase in the ability of the animals to remove oxygen at low environmental oxygen concentrations, suggesting a physiological mechanism similar to that involved in acclimation of mammals to low oxygen. The tolerance levels of small fish were similar to those of large fish at similar acclimation levels, but small fish died more quickly than large fish when exposed to lethal concentrations.

INTRODUCTION

OXYGEN LACK is often reported as a cause of death in both natural and hatchery-reared fish populations (e.g. Moore, 1942). Although many hundreds of papers have been published on responses to low oxygen among mammals (e.g. Van Liere, 1943), little work has been done to determine factors affecting the ability of fish to resist oxygen lack. For this reason, the results of the few published papers dealing with tolerance limits in fish have often been extremely variable and sometimes contradictory (e.g. Gutsell, 1929).

The present paper presents an empirical method for describing the ability of fish to withstand hypoxia and describes some of the factors affecting this ability. Although field observations have suggested that trout could adjust to a gradual lowering of environmental oxygen pressure (Jahoda, 1947; Nikiforof, 1952), experimental corroboration has been lacking. To fill this gap, a major part of the author's work was concerned with the acclimation of trout to low oxygen.

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CRITIQUE OF METHODS

Various criteria have been used by different authors to define the tolerance of fish to low oxygen pressures. For example, some have determined the oxygen pressure which caused fish to lose equilibrium within a specified period of time

(Townsend *et al.*, 1938), while others (e.g. Lindroth, 1940) determined the oxygen concentration below which the basal or standard rate of oxygen uptake could not be maintained. In many instances, these different criteria can be compared by relating the measures to the metabolism of the fish.

Molecular oxygen is essential for much of the oxidative, energy-producing metabolism of aerobic animals. As such, environmental oxygen pressure may be said to operate as a limiting factor, i.e., one which influences the metabolic rate and activities of the animal by operating as an integral part of the metabolic processes. The limiting effects of changes in oxygen pressure on the metabolic rates of fishes have been adequately demonstrated. Below a critical level, the rate of oxygen uptake is directly dependent on the oxygen pressure of the environment (e.g. Winterstein, 1908; Hall, 1929; Fry and Hart, 1948). Fry (1947) has pointed out that this dependence is expressed to its greatest extent when the animal is taking up oxygen at a maximum rate. With a further decrease in oxygen pressure, a level is reached where, respiring at its maximum rate, the animal can no longer meet the minimum requirements for cellular organization. Below this level death will occur.

The relations between supply and uptake at different levels of physical activity have received attention from Fry and Hart (1948) studying goldfish, and from Graham (1949) and Job (1954) working on speckled trout. The general relationships they describe are illustrated in Figure 1.

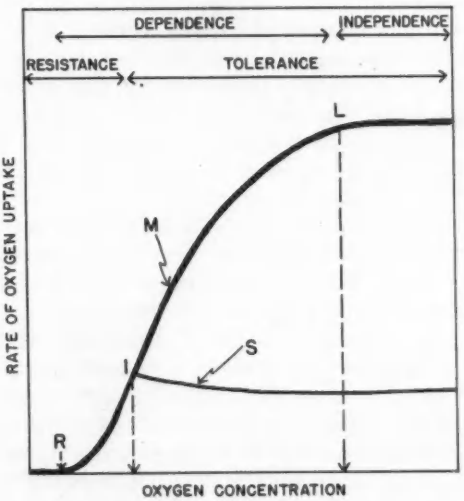

FIGURE 1. Relation between standard and active (maximum) rates of oxygen uptake at different environmental oxygen concentrations. Lines at top of graph delimit the zones of respiratory dependence and independence and the zones of resistance and tolerance. L, incipient limiting level; I, incipient lethal level; R, minimum residual level; M, maximum rate of oxygen uptake; S, standard rate of oxygen uptake.

Above a certain critical level, termed the *incipient limiting level*, the maximum rate of oxygen uptake is essentially independent of the oxygen pressure of the environment. Below this point a decrease in environmental oxygen pressure is accompanied by a decrease in the rate of oxygen uptake. Oxygen pressures above the incipient level form the *zone of respiratory independence*, while pressures below this critical point comprise the *zone of respiratory dependence*.

At a critical level in the zone of respiratory dependence, the maximum rate of oxygen uptake is reduced to a point where it is no longer sufficient to meet the minimum oxygen requirements of the animal. This level has been termed the *incipient lethal level* (Fry, 1947).

The incipient lethal level divides the range of environmental oxygen pressures into two zones; levels below the incipient lethal level constitute the *zone of resistance* while pressures above it form the *zone of tolerance*. It is perhaps appropriate at this point to distinguish between the terms *resistance* and *tolerance*. Tolerance refers to the ability of the animal to survive indefinitely under a given set of circumstances. Thus, description of the minimum tolerance of fish to low-oxygen conditions involves the determination of the lowest oxygen levels permitting indefinite survival of the fish. Resistance on the other hand refers to the ability of the animal to survive for a limited period in an environment that will eventually exert a lethal effect. The description of resistance therefore involves the determination of survival times of fish dying from oxygen lack.

Determination of tolerance limits has been approached in a number of ways by different workers. Winterstein (1908), maintaining fish in water containing a more or less constant concentration of oxygen (controlled by bubbling nitrogen through the water), determined the approximate incipient lethal level for roach (*Leuciscus rutilus*) at temperatures from 6–10°C. He noted the oxygen level which just failed to cause mortality after a week's exposure. Wilding (1939) exposed samples of blunt-nosed minnows (*Hyborhynchus notatus*) to continuous flows of water low in oxygen (produced by mixing aerated tap water and water deaerated by boiling). He determined the number of fish showing signs of asphyxia at the end of about four hours. Basu (1949), using apparatus similar to Wilding's, exposed samples of Indian carps (e.g. *Labeo rohita*) to fairly constant low-oxygen levels. He noted the length of time fish survived at various oxygen levels (the resistance time) and recorded the oxygen concentrations which just failed to cause mortality within 24 hours. Gutsell (1929) transferred speckled trout, brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*) from troughs containing aerated water into troughs containing water having low concentrations of oxygen. Using variable periods of time, he determined very approximately the levels of oxygen which just failed to cause mortality in samples of fish. Comparison between his experiments is difficult owing to variations in the time factor, oxygen levels, carbon dioxide pressures and temperatures. Unfortunately, the occurrence of disease (*Saprolegnia*) complicated some of his better controlled experiments. Townsend *et al.* (1938), Townsend and Earnest (1940) and Townsend and Cheyne (1944) exposed fingerling Pacific salmon (*Oncorhynchus* spp.), cut-throat (*Salmo clarki*) and rainbow trout to flows of water

low in oxygen. They noted the number of fish that lost equilibrium within a period of 18 to 24 hours. Herbert and Merkens (1952) carried out well-controlled experiments of the same type on rainbow trout.

Two authors conducted field experiments to determine lethal levels. Smith (1925) and Moore (1942) lowered fish in live-boxes to various depths in lakes where stagnation had produced low-oxygen conditions in the lower strata. They observed the number of fish that died within a given length of time when exposed to various low levels of oxygen. Moore's studies were carried out under both winter and summer conditions, permitting the author to compare the resistance of the fish at high and low temperatures. He stressed the importance of carrying out experiments of long duration to account for the protracted mortalities occurring at higher lethal pressures of oxygen. He found that a 24-hour period was most suitable for the summer work, whereas mortality was protracted up to 48 hours during the winter.

Several authors have attempted to determine lethal oxygen limits from metabolic data. Fry and Hart (1948) working on goldfish (*Carassius auratus*), and Graham (1949) studying speckled trout, determined at what oxygen pressure the *maximum rate of oxygen uptake* was reduced to the point where it just equalled the *standard rate of oxygen uptake*. They termed this pressure the "level of no excess activity" (see Fig. 1). Graham showed that this level was considerably higher than the incipient lethal level determined directly by measuring the lowest concentration of oxygen permitting survival. The most probable reason for this finding is that the standard rate of oxygen uptake is higher than the minimum rate of oxygen uptake required to sustain life.

Lindroth (1940, 1942) used a more direct approach to estimate the incipient lethal level (termed by Lindroth the "critical pressure") from oxygen uptake data. For roach and pike (*Esox lucius*) he determined the oxygen pressure below which the metabolic rate of quiescent fish (the standard rate of oxygen uptake) was reduced as a consequence of a decrease in the environmental oxygen pressure.

Lozinov (1952) studied the respiration of several European fishes including the sturgeons *Acipenser güldenstadti* and *A. stellatus*. He followed the rate of oxygen uptake of fishes held in closed containers, where the environmental oxygen pressure was being continually lowered by the animals' respiration. He noted that in the lower region of the zone of respiratory dependence the rate of oxygen uptake fell off, and he postulated that the point of flexure represented a division between zones of survival and mortality.

From the data presented, it would seem that Lozinov was observing a curtailment of oxygen uptake occurring after the fish had been in the zone of resistance for some time. In this case his determination of the "level of no excess activity" would tend to be lower than the true incipient lethal level. A paper by Privolnev (1947), describing similar experiments on species other than sturgeon, was cited by Lozinov.

Several authors have determined the pressure of oxygen present after a fish has been asphyxiated in a sealed vessel. This concentration has been termed the

"*residual level*" by Irving *et al.* (1939). Theoretically this level could have any value from zero mm.Hg.O_2 to the incipient lethal level (see Fig. 1). Where the volume of water is large in comparison to the amount passing through the gills of the fish, the value may approximate the incipient lethal level. When the volume of water in the container is relatively small, and where the fish reduces the oxygen concentration rapidly, the observed residual level can be postulated to represent the pressure at which the circulatory system can no longer provide oxygen to the cells. This value would be determined by the characteristics of the blood pigments and the sensitivity of the nervous centres controlling respiration and circulation. In theory, as long as individual cells continued respiring, an equilibrium would be established through diffusion and the final pressure remaining in the water would be zero mm.Hg.O_2. In practice the value is found to be higher. With intermediate volumes of water, the residual level may have any value between this minimum residual level and the incipient lethal level. Data on the possible relations of the minimum residual level to rate of metabolism and to resistance will be outlined in a later section (p. 424).

In studies of the effects of carbon dioxide on the asphyxia of fish, Fry, Black, and their associates have determined approximate minimum residual levels of oxygen for a number of species including speckled trout, rainbow trout, Kamloops trout (*Salmo gairdneri kamloops*), and kokanee or land-locked sockeye salmon (*Oncorhynchus nerka kennerlyi*) over a wide range of CO_2 tensions (Fry, 1939; Fry and Black, 1938; Irving, Black and Safford, 1939; Hart, 1945; Fry, Black and Black, 1947; Black and Black, 1951). Wiebe *et al.* (1934) determined residual levels for several fishes, including the steel-coloured shiner (*Notropis whipplei*). Powers (1922) and Safford (1940) determined residual levels for several marine species.

A number of experiments often quoted in the earlier literature (see bibliography in Gutsell, 1929) involved the asphyxiation of fish in limited volumes of water. The work of Paton (1903) is typical of these early experiments.

Several Russian workers, including Lozinov (1952), determined residual levels (probably higher than the minimum residual level) for several fishes. The most extensive work was done on sturgeon.

Other authors have studied the asphyxiation of fish in containers of large size or in containers supplied with flows of water insufficient to overcome the oxygen-depleting effects of the animals' respiration (e.g. Wilding, 1939). The results of these experiments are difficult to interpret, for the residual levels obtained were dependent on the relation of the metabolic rate of the fish to the volume of water present in or passing through the container; and this relationship is empirical.

Gardner and Leetham (1914) and Gardner and King (1922) conducted experiments to determine residual levels for brown trout and goldfish. Before placing fish in the experimental containers (45-litre flasks), they removed some of the oxygen by bubbling nitrogen and oxygen mixtures through the water. They determined the oxygen level at which the fish lost equilibrium ("asphyxial level"). Since the volumes of their containers were relatively large and some

circulation of the water was allowed, when the oxygen reached a low level it became relatively constant (i.e. the effects of limited respiration of the fish at very low oxygen concentrations tended to be counteracted by the small introduction of aerated water). In some experiments no mortality occurred even after several days' exposure. Thus, even though the initial period of exposure was accompanied by a changing oxygen level, the residual level was determined under fairly constant oxygen conditions. In this case the "asphyxial level" obtained would lie closer to incipient lethal level than the minimum residual level.

In connection with fish cultural procedures experiments have been performed to determine the maximum loads of fish that can be safely transported in various types of carrying tanks. The usual procedure has been to note the oxygen pressure remaining after some or all of the fish show distress from oxygen lack (the oxygen pressure is the container being reduced by the respiration of the fish). As these experiments usually involve relatively large quantities of water, the final level is probably somewhat above the minimum residual level. The relatively high levels obtained in these experiments corroborates this view. Experiments performed by Chapman (1938) and Prévost and Piché (1939) are of this type.

When an animal is exposed to oxygen levels within the range of pressures between zero mm.Hg.O_2 and that of the incipient lethal level, death occurs. The time taken from the initial exposure to the lethal conditions until death occurs (the resistance time) was recorded for a number of the experiments reported above (e.g. Graham, 1949; Wilding, 1939). Wells (1913) and Keys (1931) conducted extensive studies on the resistance of fish to hypoxia. Scattered references to resistance times at various constant levels of oxygen (e.g. Pearse and Achtenberg, 1920; Packard, 1905, 1907, 1908; Paton, 1903) are numerous in the literature. In some of the experiments cited above resistance times for various changing levels of oxygen have been noted, (e.g. Wilding, 1939; Chapman, 1938). These determinations are empirical and in most cases cannot be related directly to the metabolic pattern of the fish.

From the foregoing survey of literature, it is evident that several different criteria have been used to describe the ability of fish to "tolerate" hypoxia. The fact that most of these criteria are not equivalent has sometimes been overlooked. The oxygen pressure at which fish exhibit respiratory distress (e.g. Wilding's experiments, 1939) is higher than the pressure causing fish to lose equilibrium (e.g. Townsend's experiments, 1938, 1940, 1944). This pressure is in turn greater than the level at which short-term lethal effects are noted (e.g. Graham's experiments, 1949) and even higher than the pressure observed when fish die in closed chambers (e.g. Lozinov's experiments, 1952). In spite of the differences, all these pressures have been described as low-oxygen tolerance levels for fish. To provide a consistent method of comparing the tolerance of various fishes it is essential to adopt a standard experimental procedure in which a well-defined criterion of tolerance is established. In the present paper the pressure which just failed to bring about 50% mortality in a sample of fish was used to define tolerance. The length of time fish survived at constant lethal levels of oxygen was

also determined to describe the response of the animals under severe hypoxic conditions. In the following section, the experimental procedure is outlined in detail.

MATERIALS AND METHODS

Care and Maintenance of Fish

Fish used in experiments were fry and fingerling speckled trout obtained in spring and early summer from the Ontario Department of Lands and Forests hatchery at Chatsworth. The hatchery water temperature was reasonably uniform during the period fish were being taken for experiments, varying between 8.0° and 10.5°C. A single series of observations on the oxygen concentration of the Chatsworth water showed that at the prevalent temperature of 8.5°C. the water contained 9.10 mg.O_2/l. (78% of air saturation). Fish were transported from the hatchery to the Laboratory for Experimental Limnology at Maple, Ontario, with negligible losses. Prior to experiments, the fish were kept in outdoor cement retaining tanks (capacity 525 liters). These tanks were supplied with running water which contained approximately 7.0 mg.O_2/l. (approximately 60% saturation, depending on the temperature of the water). The annual variation in the temperature of this water was from 7.0°C. (in December) to 10.2°C. (in July). In preparation for experiments, the fish were moved into indoor retaining tanks (capacity 15 to 333 l.). The temperature of these tanks was maintained at 8.5 $\pm$0.3°C., while the oxygen content of the water was varied according to the type of experiment being conducted.

From July, 1950, to February, 1951, the fish were fed a pork liver diet supplemented with brewers' yeast. Once weekly a mixture of 50% beef liver and 50% pork liver was fed. For a period of three weeks in November, 1950, the diet was changed to uncooked smelt supplemented with brewers' yeast and cod liver oil. Like many freshwater fish, uncooked smelt contains an anti-vitamin B factor which creates a vitamin B-1 deficiency when used as fish food (Wolf, 1942). This fact was not appreciated until extensive mortality had occurred in adjacent troughs where samples of fingerling lake trout (*Salvelinus namaycush*) were being held. Resumption of the original pork liver regimen rapidly ended the lake trout mortality. Lethal oxygen data obtained during the smelt feeding period were discarded. From March to July, 1951, a commercial fish food was used ("Red-gil", prepared by the Burns Packing Company, Calgary).

The frequency of feeding varied according to the size of the fish. The smallest fish used were approximately 3.3 cm. in length. These fish were fed four times daily, six days a week. When the fish reached a length of approximately 4 cm. the frequency of feeding was reduced to twice daily, and when they reached 5 cm., they were fed once daily.

Fish used in experiments were observed to be vigorous and healthy. Their growth was similar to that noted in the hatchery stock from which they were obtained. On two occasions the stocks of fish became infected with *furunculosis*. All diseased fish were destroyed. A proportion of all fish received from the hatchery suffered from fin rot (restricted to the dorsal fin). This affliction, how-

ever, had no apparent effect on the vigour of the animals. Data on the size of fish used in experiments are summarized in Table I.

Lethal Oxygen Experiments

For the present experiments it was necessary to develop techniques more sensitive than those required to discern gross differences in the low-oxygen resistance and tolerance of different species (Basu, 1949) or of the same species tested at different temperatures (e.g. Graham, 1949). The range of oxygen pressures over which a graded effect in mortality could be observed was relatively narrow. Regardless of acclimation history or state of activity, all groups of trout studied survived for at least 5 days when exposed to flows of water containing over 1.9 mg.O_2/l. at 9°C. (17% of air saturation). On the other hand all fish tested at oxygen concentrations below about 0.5 mg.O_2/l. at 9°C. (5% of air saturation) died at a more or less uniform and rapid rate. Thus at 9°C. the entire range of oxygen resistance, between the extremes of no mortality on the one hand and almost instantaneous death on the other, lies in the narrow interval of 1.4 mg.O_2/l. Within this interval the effects of acclimation, growth and activity on the resistance of the fish are expressed through alterations in resistance times and in incipient lethal levels.

Experiments were conducted by exposing samples of from 7 to 12 trout, in 250 to 6,000 ml. Erlenmeyer flasks, to flows of deoxygenated water and noting the time elapsing between the imposition of the low oxygen and the cessation of the respiratory movements. Fish were placed in the flasks from 30 minutes to 24 hours before introduction of deoxygenated water. During this preliminary period, the flasks were provided with flows of water with oxygen concentrations approximately the same as those in the acclimation baths. The latter were designed to carry flowing water of controlled oxygen content. The effects of varying the duration of the preliminary pre-exposure period on the mortality of the fish are discussed in a later section (p. 397).

The concentration of oxygen in the water used in lethal experiments was maintained at a constant level by use of a fractionating column similar to that described by Fry (1951). A modification of this apparatus was designed to produce larger volumes of deoxygenated water (Fig. 2). Aerated tap water was introduced into a constant-level cylinder at the top of the apparatus. From here the water fell at a constant rate through two long cylinders filled with glass marbles. The purpose of the marbles was to increase the surface area of the water exposed to the atmosphere within the cylinder. Nitrogen was passed upwards through the two cylinders, escaping through a small aperture at the top of the upper cylinder. The oxygen-deficient water arriving at the base of the cylinders passed through rubber tubing to another levelling cylinder from where it flowed at a constant rate to the flasks containing the fish.

With a constant volume of water passing through the apparatus, the oxygen concentration of the water could be varied either by changing the amount of nitrogen introduced or by altering the height of the lower levelling cylinder, thereby altering the distance the aerated water fell through the reduction

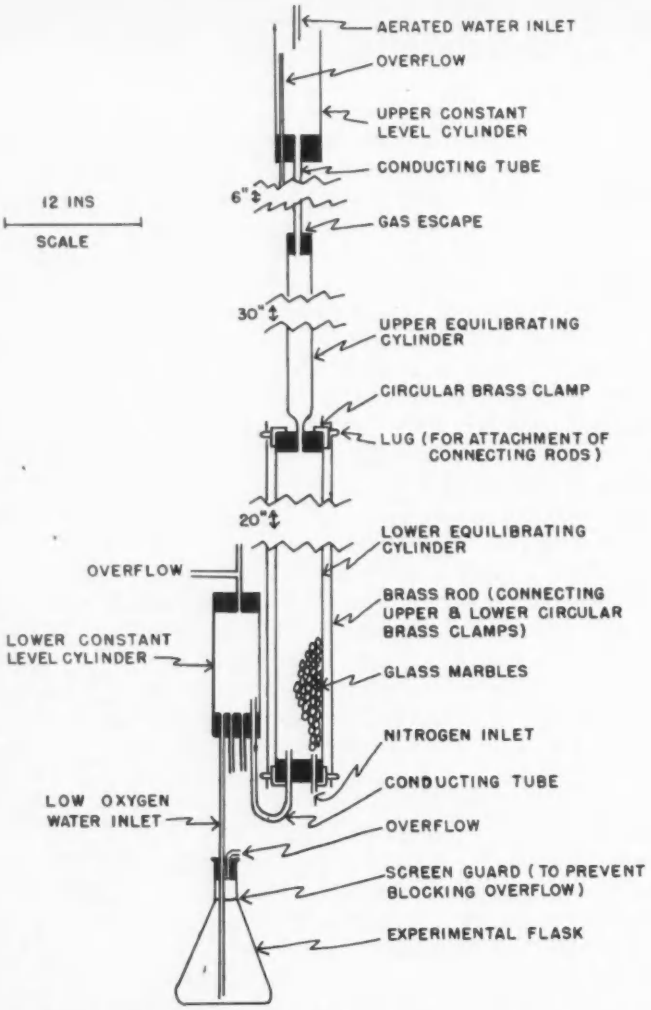

FIGURE 2. Apparatus for reducing the oxygen concentration of water.

cylinders and thus changing the amount of equilibration taking place between the water and the nitrogen-high cylinder atmosphere. When water was passed through the apparatus at a rate of approximately 3.5 l./min., with a nitrogen flow rate of approximately 50 cc./min., the oxygen content of the water was reduced from 5.00 to 0.35 mg.O_2/l.

The rate of water flow through the flasks was varied according to the size and number of fish used. In selecting a flow rate two factors had to be considered. First, the rate of flow had to be sufficient to overcome the oxygen-depleting

effects of the fishes' respiration. Second, at the start of each experiment it was desirable to flush the experimental chamber as rapidly as possible. This was especially important in experiments where mortality took place rapidly, for if the rate of replacement was slow, then the mixing period formed a relatively large part of the total period of exposure of the fish. The starting time for each experiment was arbitrarily taken to be that time when the oxygen content had reached 2.0 mg.O_2/l. In most experiments the period of mixing was under 10 minutes, the most frequently recorded time being 3 minutes. However, in the first series of experiments performed on young fingerling trout, using the unmodified apparatus described by Fry (1951), the duration of mixing was longer, averaging 20 minutes.

At the beginning of experiments, from 3 to 5 successive analyses of the oxygen content of the water flowing from the experimental flasks were made to determine the starting time of each experiment (i.e. when the oxygen content of the water reached 2.0 mg.O_2/l.). After the oxygen content had become constant, from 3 to 35 determinations (depending on the duration of the experiment) of the oxygen content of the effluent water were carried out to keep a check on the constancy of the oxygen level. In approximately 95 cases out of 100, an individual oxygen determination fell within $\pm$ .07 mg.O_2/l. of the mean value (see Table II).

Observations on the numbers of fish succumbing to low oxygen were carried out more or less continuously during the first 12 hours of the experiment. From then until the end of the first day the frequency of observations was reduced to intervals of no more than 2 hours. In experiments lasting more than 24 hours, the intervals between observations were increased further; from 08:30 hours to 24:00 hours observations were made at intervals of no more than 3 hours.

In all the lethal experiments the fish were subject to stimulation caused by changes in the room lighting, by manipulations involved in sampling water flows for oxygen content, and by other external factors. The possibility that such stimuli might have excited the fish and raised their demand for oxygen to a higher point than if the stimuli were absent prompted a series of experiments to test the effects of external factors on resistance. Another problem that required clarification was concerned with the length of time fish should be held in experimental flasks before introduction of low-oxygen water. Graham (1949) placed fish in flasks for a minimum of 12 hours before each experiment began. Since it was desirable to reduce this period to make the fullest use of the apparatus in the time available, it was considered necessary to determine the effects on resistance of varying the pre-exposure period.

To study the problems outlined above, the following experiment was performed. Three samples of fingerlings 9 months old were taken from an acclimation bath (acclimation level 7.09 mg.O_2/l.) for each experiment. One sample was placed in a flask in a dark chamber, while a second sample was introduced into a flask exposed to ordinary room lighting conditions. Both flasks were supplied with flowing tap water. Twenty-four hours later low-oxygen water was introduced and the resistance times of the fish determined. The third sample of fish was placed

in an experimental flask, in the light, just 30 minutes before the flow of deoxygenated water was started. By comparing the resistance times of the three groups over a wide range of lethal levels, the effects of external stimuli and of the duration of the pre-exposure period could be studied. All experiments (except at very low oxygen levels) were started at midnight, when the metabolic rate of the fish held in the dark chamber was probably approaching a minimum value (e.g., see Graham, 1949). Observations on the dark-tested fish were made with a shielded flashlight.

Experiments on the Active Metabolic Rate

Measures of the active metabolic rate of trout were obtained using the apparatus designed by Fry and Hart (1948). Experiments involved placing fish in an annular chamber which was rotated at a rate sufficient to keep the fish swimming at a maximum steady rate. In the present research, to carry out several tests simultaneously, fish were placed in 3 to 6 Erlenmeyer flasks (size varying from 125 to 1,000 cc., depending on the size of fish used) immersed in the annular chamber. To determine the rate of metabolism at different oxygen pressures the flasks were supplied with water piped from the deoxygenating column. After fish had remained in the flasks for 15 minutes, a sample of the water flowing through each flask was analysed to determine the oxygen concentration. The water flow was then stopped and the annular chamber rotated to keep the animals active. After the oxygen content of the water had been reduced by approximately 1.5 mg.O_2/l., the machine was stopped and a sample of water withdrawn for analysis. The procedure was then repeated from 2 to 4 more times until a more or less constant value was obtained for the metabolic rate.

Job (1955) compared values for the maximum rate of oxygen uptake obtained by the author (using the flask method) with his own data (determined by using the unmodified rotating chamber apparatus). In the zone of dependence, uptake values obtained by the two methods were similar. Even when the fish were confined to flasks and not actively swimming against the current, they maintained a high rate of oxygen uptake. However at higher oxygen levels (i.e. above about 7.0 mg.O_2/l.) it was difficult to obtain consistently high values for the metabolic rate. Excepting the oxygen level, experimental conditions were the same for all experiments where the flask method was used. Thus, depression of environmental oxygen level, *per se*, may have been an important factor in stimulating the fish to activity in experiments conducted at lower oxygen concentrations.

The rate of oxygen uptake became relatively constant after the animals had been in the flasks for about 30 minutes. To illustrate this, two experiments were conducted to determine the oxygen uptake of fish over a 5-hour period. After the first reading the rate approached a relatively constant value, not differing from the mean rate of uptake by more than 6%.

Acclimating Methods

To study the effects of low-oxygen acclimation on the resistance and active metabolism of young speckled trout, a number of acclimation baths supplied

with flows of deaerated water were set up. The low-oxygen water was provided by mixing tap water with water from an equilibration column.

The oxygen levels in the acclimation baths were established empirically by adjusting the flows of tap and low-oxygen water. In cases where fish were being acclimated to oxygen levels above that of the tap water (i.e. above approximately 7.0 mg.O_2/l.) the water was aerated by bubbling compressed air through the tanks. As it was necessary to maintain relatively large numbers of fish in each bath, respiration of the fish had a noticeable influence on the concentration of oxygen in the baths. This was specially evident in experiments involving larger fish. For this reason acclimation levels were more variable than lethal levels; the average standard deviation of the oxygen content in the baths was $\pm$ 0.33 mg.O_2/l., as compared with 0.035 mg.O_2/l. in the lethal flasks.

Chemical Analyses

Determinations of dissolved oxygen concentrations were made using the unmodified Winkler method (Ellis *et al.*, 1946). Tests conducted throughout the experiments showed that there was no interference due to inorganic ions (e.g. ferrous iron) or accumulated organic wastes.

A complete chemical analysis of the water supply of the laboratory was made in 1947, and has been reported by Brett (1952).

Statistical Procedures for Lethal Oxygen Experiments

When young trout are exposed to severe oxygen lack, a typical mortality pattern is observed. This pattern is similar to that recorded in other studies involving time-effect relations in animals; e.g., in bioassay work (Bliss, 1952), in studies of the lethal temperature relations of fish (Fry *et al.*, 1946), and in one case, in experiments on the resistance of fish to hypoxia (Herbert and Merkens, 1952). At very low concentrations of oxygen, mortality occurs rapidly; the time intervals between successive deaths within the sample are quite uniform. At higher concentrations of oxygen, a few deaths may occur near the beginning of the experiment, but the greatest part of the mortality occurs after a considerable time lag. The interval between successive deaths, during this latter period of mortality, increases as the experiment continues. In the higher range of oxygen concentrations the same pattern occurs, but the total mortality at the end of the 5,000-minute experimental period is incomplete with some fish still surviving. Finally an oxygen concentration is reached which causes no mortality at all during the experimental period. The general relationships are illustrated in Figure 3 and the data summarized in Table III. Curve A shows an experiment in which mortality occurred rapidly and uniformly throughout the experiment. Curve B illustrates a case where 100% mortality occurred, but where the intervals between successive deaths increased throughout the experiment. The second group of data forms the typical asymmetrical sigmoid curve noted in many experiments where animals are exposed to lethal conditions. Curve C shows a case where only 40% mortality occurred in 5,000 minutes.

When the data in Figure 3 are replotted with mortality expressed in terms of units of the standard deviation (probits) and the resistance times are trans-

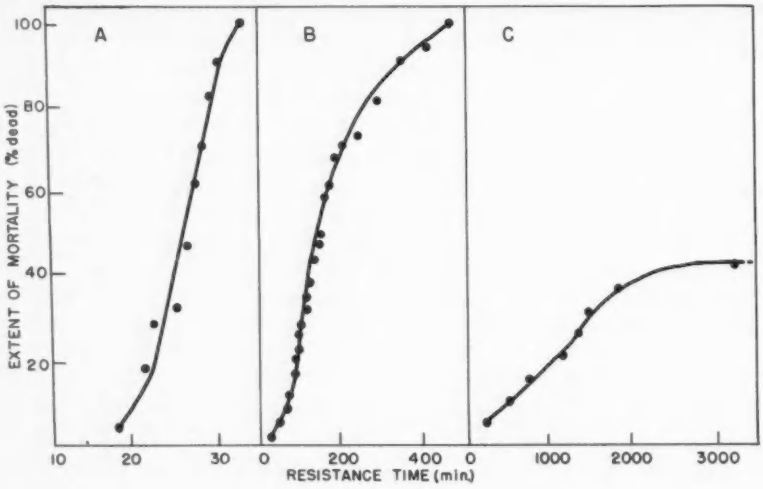

FIGURE 3. Resistance times of young speckled trout at different lethal oxygen concentrations. A, large fingerlings at 0.39 mg.O_2/l.; B, fry at 1.25 mg.O_2/l.; C, large fingerlings at 1.55 mg.O_2/l.

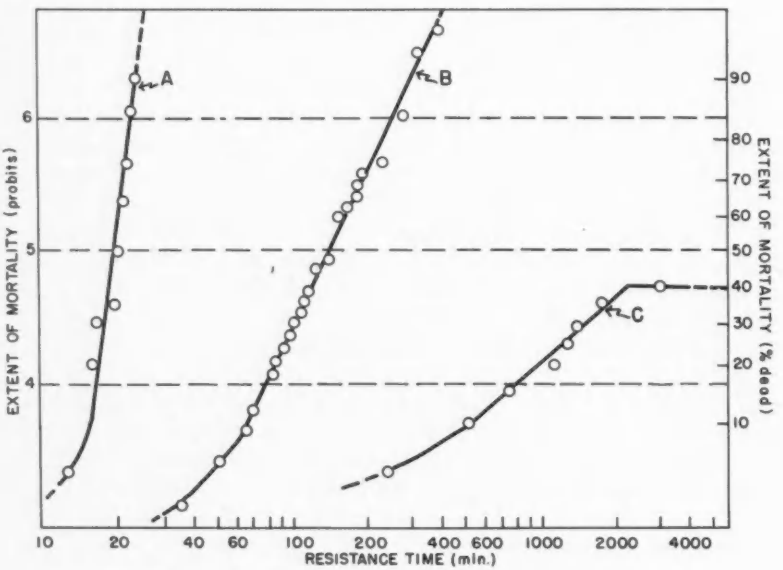

FIGURE 4. Log-probit plot of data presented in Figure 3.

posed into logarithms of time, the points can be resolved into approximate straight lines (Fig. 4). The fit is most exact in the mortality range between 4 and 6 probits (i.e., between 16 and 84% mortality).

It will be noted that the slopes of the lines tend to decrease as the resistance times increase. This systematic change in variability is discussed in detail on page 406.

As the logarithms of resistance times of individuals in samples tend to be distributed normally, the best calculated estimate of the time to 50% mortality (ET_{50}) is the geometric mean time to death. However as there is no resistance time recorded for zero % mortality, the recorded range of resistance times is asymmetrical with respect to the median, one more observation being made in the mortality range from 50 to 100% than in the range from zero to 50% mortality. Thus, in making the calculation the last resistance time must be omitted.

To confirm the view that a log-normal relationship exists, three different mean values of resistance times were calculated for a series of 25 experiments selected from the entire body of data according to a random number table. These three were the arithmetic, geometric and harmonic means, omitting the last recorded resistance time. The results showed that the geometric mean was the derivative closest in value to the observed median time to death, while the harmonic mean was consistently below, and the arithmetic mean consistently above the observed time to 50% mortality. Statistical tests showed that the arithmetic and harmonic means were significantly different from the median while the geometric mean was very close to the observed median value (see Table IV). Thus, of the derivatives tested, the geometric mean resistance time (omitting the last resistance time observed) was the most exact estimate of the time to 50% mortality of a sample.

The graphic methods of Litchfield (1949), involving interpolations from log-probit plots similar to Figure 4 (curves A and B), have been used to estimate the geometric mean time to death. Because the slope of the time-percent effect curve (expressed in log time per probit) is an estimate of the standard deviation of the resistance times within experiments, calculation of slope provides a measure of dispersion. As the methods described by Litchfield do not require the transposition of the original data into logarithms, an arithmetic function of the standard deviations of the logarithms of the resistance times is used instead of the actual standard deviation. This function, termed "S" (the slope function), is the anti-logarithm of the standard deviation of the log times to death.

These statistics, calculated for each experiment in which 50% or more mortality occurred, were used to determine whether or not significant differences existed between the times to 50% mortality in samples of fish of different ages, and of fish subjected to different treatments. In essence, the method involves the comparison of the logarithms of the times to 50% mortality of two experiments, using the standard errors of the logarithms of the resistance times as measures of the dispersion within experiments.

Incipient lethal levels (the oxygen concentrations at which 50% mortality occurs during the experimental period of 5,000 minutes) were computed accord-

ing to the methods described by Litchfield and Wilcoxen (1949). The procedure is essentially similar to that described above for calculating the times to 50% mortality and the variability within experiments. Figure 5 represents a typical plot of data used to compute incipient lethal levels; here the percentage mortality, noted at the end of the 5,000-minute experimental period (expressed in probits), is plotted against the logarithm of the oxygen level at which the experiment was conducted. As in the graphic determination of the median resistance time, the incipient lethal level (ED_{50}) is determined by interpolation and S, the slope function, is calculated.

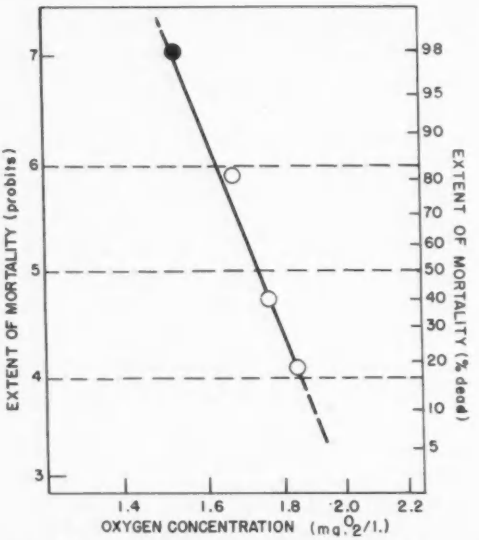

FIGURE 5. Extent of mortality occurring within 5,000 minutes in samples of fry acclimated to 10.50 mg.O_2/l. and exposed to various lethal oxygen levels. *Open circle* indicates experiment in which less than 100% mortality occurred; *solid circle* indicates experiment in which 100% mortality occurred and in which a corrected value was calculated using the method described by Litchfield (1949).

Eisenberg (1952) evaluated the results of 52 pharmacological dose-effect experiments and concluded that the values of ED_{50} and S, estimated by the Litchfield-Wilcoxen graphical method, were in good agreement with the corresponding statistics obtained by numerical computation.

As a test of experimental technique, a number of replicate experiments on resistance were conducted. These experiments (listed in Table V) involved fish of all age groups and most acclimation levels studied. A "significant" difference between replicates occurred only once and as it was only just at the 95% confidence level, it was probably a chance effect. In general there was good agreement between replicates.

Statistical Methods in Experiments on Active Metabolic Rate

The metabolism of fish is influenced by many factors, both environmental and intrinsic. When studying the effects of a specific factor on the metabolic rate of fish, there is a danger that if the effect is not great, then the variability contributed by physiological differences between fish and small variations in experimental procedure may mask the effect so that it cannot be recognized clearly. In cases such as these, analysis of variance techniques (Snedecor, 1946) are valuable for attributing the variability observed in an experiment where responses to different treatment are being tested, to the predictable sources of variation.

In measuring the active metabolic rates of trout acclimated to different oxygen levels, it became apparent that the effects of acclimation were not great, considering the total variability inherent in the experiments. By redesigning the experiment (p. 398), simultaneous comparisons between experiments and replications within the experiments were possible. These improvements in design permitted a more precise comparison of effects through analysis of variance. Determinations were made of the total variability due to differences in the acclimation levels of the fish, size of fish, between replications, and finally to the influence of uncontrolled factors contributing to experimental error. This separation of effects eliminated much of the masking noted in the preliminary experiments.

LETHAL OXYGEN EXPERIMENTS

Behaviour of Fish During Lethal Oxygen Experiments

A typical behaviour pattern was observed when young speckled trout were exposed to flows of water low in oxygen. When experimental flasks were supplied with well-aerated water, the fish remained relatively quiescent, individuals making a few exploratory movements and occasionally "surfacing" (i.e. moving to the neck of the flask). The mechanical procedures involved in introducing low-oxygen water had little effect on the behaviour of fish. If a disturbance was caused, it was immediate and short-lived. Introduction of oxygen-deficient water, however, resulted in a violent burst of activity involving all the individuals in the sample. In contrast with the occasional burst of activity associated with mechanical manipulation, increase in activity due to low oxygen lasted longer and occurred only after the oxygen level had dropped to a near-lethal level. These responses are similar to those of sticklebacks, minnows and brown trout fry as described by Jones (1952). Attempts to surface were evident. Movements of the fish became uncoordinated a few minutes after initial exposure to the lethal conditions; many of the fish suffered a temporary loss of equilibrium. At higher lethal concentrations many of the fish recovered their balance, and remained quiescent at the bottom of the flask, activity being restricted to laboured respiratory movements and efforts to maintain an upright position. The fish underwent a second loss of equilibrium which, in almost every case, was followed by a cessation of respiratory movements (within 20 to 200 minutes of collapse). Approximately 10 minutes before the collapse of respiration, some of the animals executed violent and uncoordinated "leaps".

At lower lethal oxygen concentrations, where mortality proceeded rapidly throughout the sample (e.g. where mortality was complete within 45 minutes), the substantial increases in activity and surfacing, followed by a loss of equilibrium noted in the previous long-term experiment, were observed. However, there was no temporary recovery from the first loss of equilibrium; death occurred very shortly after the initial collapse.

On exposure to hypoxic conditions the depth of breathing increased, the opercula described wider arcs and the movements of the jaws and of the floor of the mouth became exaggerated. Following cessation of respiratory movements the opercula fanned out and the mouth opened to its widest extent.

Relation between Resistance, Tolerance and Oxygen Level

The data presented in this section illustrate the empirical relationships between resistance, tolerance and environmental oxygen level.

(i) resistance time and lethal oxygen level

In general the resistance of young trout to low oxygen varies directly with the oxygen concentration of the environment. At very low concentrations mortality occurs rapidly. Above this range resistance times increase at a progressively greater rate, until an oxygen level is reached where less than 50% mortality occurs; i.e., where the median resistance time is, in theory, infinitely long.

The results of a typical series of experiments are illustrated in the log-probit plots composing Figure 6, Table VI. In these experiments a series of resistance times for various lethal oxygen levels, and the incipient lethal level were determined for a group of speckled trout fry acclimated to 10.50 mg.O_2/l. All stages of mortality mentioned above, from rapid complete mortality to gradual incomplete mortality, are represented in the series.

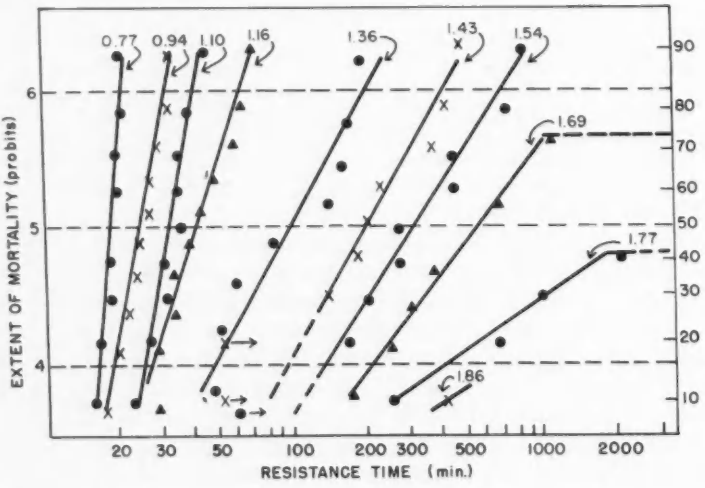

Figure 6. Resistance times of fry acclimated to 10.50 mg.O_2/l. at various lethal oxygen levels. Lethal levels, in mg.O_2/l., indicated by figures in body of graph.

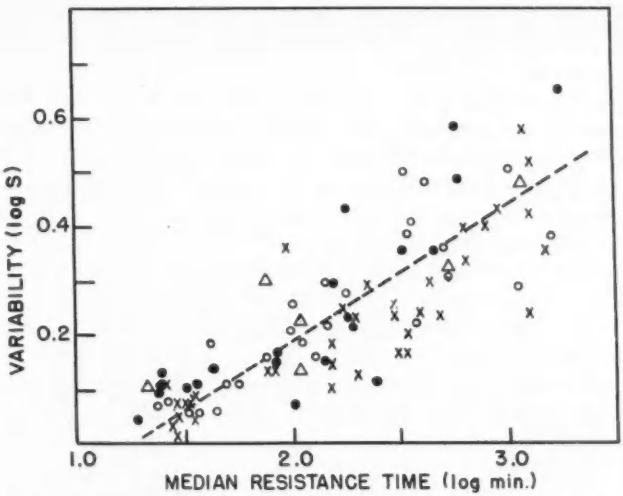

FIGURE 7. Increase in variability related to increase in resistance time. *Solid circle*, experiments on fry (Series E); *open circle*, experiments on small fingerlings (Series A); *open triangle*, experiments on small fingerlings (Series G); *cross*, experiments on large fingerlings (Series C).

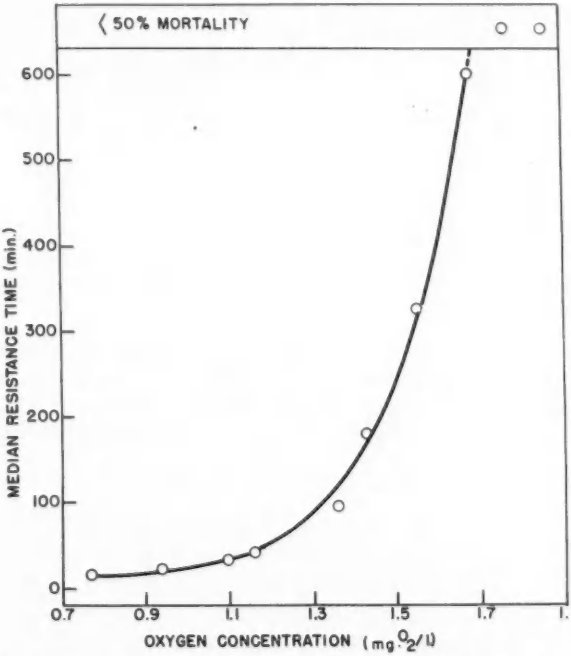

FIGURE 8. Median resistance times at various lethal oxygen levels in fry acclimated to 10.50 mg.O_2/l. Points in box at top of graph indicate results of experiments in which less than 50% mortality occurred.

It is of note that as the oxygen level of the experiments increased, not only did resistance times increase, but also variability within experiments (as indicated by the slopes of the lines) became greater (see Fig. 6). In Figure 7 the slopes of the log-probit lines are plotted against median resistance time for four series of experiments involving fish of three different ages and 13 different acclimation levels. The positive correlation between these two statistics indicates that the pattern illustrated in Figure 6 is a general trend throughout the data. Thus, the longer an experiment lasts, the greater the variability within the experiment tends to be.

When plotted against lethal oxygen level, median resistance times derived from the data presented in Figure 6 fall along a sharply breaking curve (Fig. 8). If the data are replotted with the median resistance times on a logarithmic scale, a linear relation exists over two-thirds of the range of oxygen concentrations tested (Fig. 9). Below approximately 1.15 mg.O_2/l. the median resistance times were apparently longer than might be expected from an examination of the remainder of the data. The flexure at approximately 1.15 mg.O_2/l. can be explained if it is assumed that median resistance times approach a constant

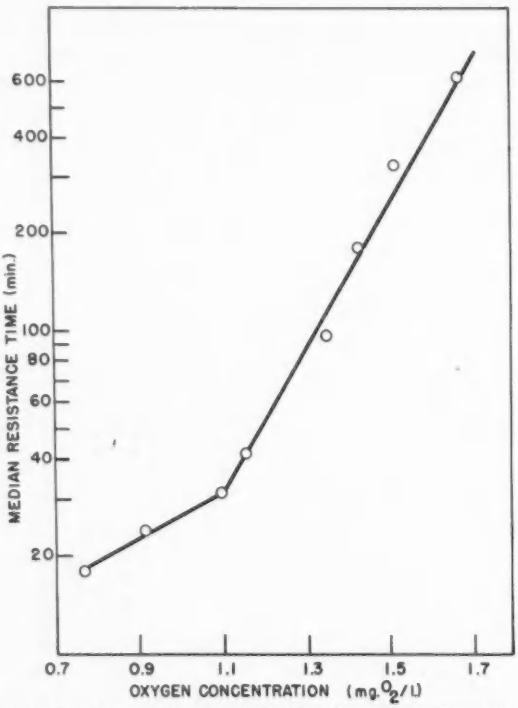

FIGURE 9. Median resistance times at various lethal levels in fry acclimated to 10.50 mg.O_2/l. Semi-logarithmic plot of data presented in Figure 8.

minimum value at low oxygen pressures. It will be noted in Figure 8 that at low oxygen levels the median resistance time approaches an asymptotic value. Evidence of the fact that such curves become asymptotic may be derived from examination of other resistance curves presented later (e.g., see Fig. 14, 15, 16). In the fry experiment under consideration, this "minimum resistance time" would be approximately 15 minutes. If this value is subtracted from each of the median resistance times shown in Figure 8, and the revised data replotted on semi-logarithmic paper (see Fig. 10), a straight line is obtained at lethal levels above that at which median resistance times approach a minimum.

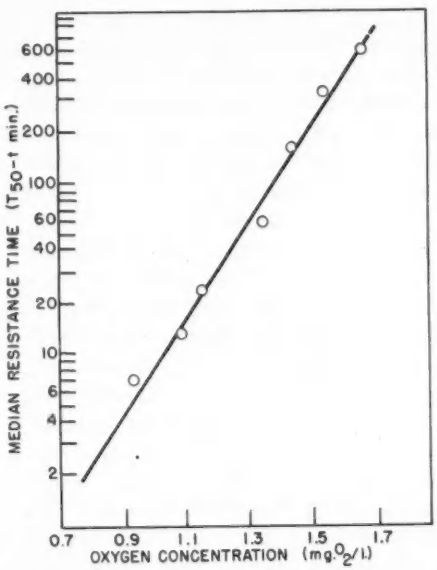

FIGURE 10. Median resistance times at various lethal oxygen levels in fry acclimated to 10.50 mg.O_2/l. (modified semi-logarithmic plot of data presented in Figure 8—see text).

In general, in the oxygen concentration range between the level at which the resistance times are at a minimum, and the incipient lethal level, the relation between median resistance times and oxygen level tends to be semi-logarithmic. The formula for this relation is:

$$\log (T_{50}-t) = \log a + bX \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where X = lethal oxygen level (mg. O_2/l.)
T_{50} = median resistance time (minutes)
t = minimum resistance time (minutes)
a = value of $(T_{50}-t)$ when $X = 0$
b = regression of $\log (T_{50}-t)$ on X.

The regression formula for the data concerning fry acclimated to 10.50 mg.O_2/l. is:

$$\log (T_{50} - 15) = -0.977 + 2.23\ X$$

The standard error of the regression coefficient (s_b) is 0.088.

(ii) TOLERANCE AND OXYGEN LEVEL

The range of oxygen concentrations in which only partial mortality occurs within a sample, is quite narrow. In the case of the fry experiment illustrated in Figures 6–10, all the animals died at 1.50 mg.O_2/l., whereas at 1.86 mg.O_2/l. (0.36 mg.O_2/l. higher) only 20% mortality had occurred at the end of 5,000 minutes. The percentage mortality occurring within 5,000 minutes is related to oxygen concentration in Figure 5. In this experiment the incipient lethal level was estimated to be 1.75 mg.O_2/l.

Two other lethal levels are of practical importance; these are the levels at which all but the most resistant fish die within the 5,000 minute period and the level at which all but the most susceptible fish live for a minimum of 5,000 minutes. Determination of the oxygen levels which bring about 5%, 50% and 95% mortality in 5,000 minutes provide a basic description of the tolerance of the group of fish under consideration. In the experiment under consideration, the level at which 95% of the fish would die within the experimental period was calculated to be 1.50 mg.O_2/l. with 95% fiducial limits of 1.56 and 1.46 mg.O_2/l. The level at which only 5% of the population would die during the same time was 1.93 mg.O_2/l. with 95% confidence limits of 2.04 and 1.79 mg.O_2/l. The calculations were made according to the method outlined by Litchfield (1949).

The choice of 5,000 minutes as the maximum duration for experiments was based on the fact that the immediate lethal effects of low oxygen stress are probably complete before that time. Implicit in the design of the experiments, the median resistance times could have any value up to 5,000 minutes. In only three cases in the entire series of experiments did median resistance times exceed 2,000 minutes. These three cases occurred in a special group of experiments in which the effect of activity on resistance was being studied. These represent rather particular circumstances (see p. 418) and cannot be considered typical. Thus the immediate lethal effects of oxygen lack probably occurred within the 5,000-minute experimental period. There is little doubt that longer exposure would have caused additional mortality in many cases. However, these mortalities would probably have been due to secondary results of oxygen lack rather than to immediate lethal effects. Brett (1952) has presented a rationale for the selection of a 10,000-minute experimental period in the study of thermal resistance in young Pacific salmon. Many of his points are applicable in the case of a 5,000-minute test period for experiments on low-oxygen resistance.

Effects of Acclimation on Resistance and Tolerance

In the previous section the basic resistance and tolerance patterns observed when young trout are exposed to low-oxygen conditions have been outlined. It is in terms of these basic response patterns that the effects of acclimation, growth

and metabolism on resistance and tolerance have been studied. In the following section, experiments dealing with acclimation to low-oxygen conditions are described. The criteria used for characterizing the acclimation process are alterations in median resistance times and incipient lethal levels.

(i) RATE OF GAIN OF ACCLIMATION TO LOW-OXYGEN CONDITIONS

When young trout were transferred from water containing a high concentration of oxygen to water with a low (but not lethal) concentration, a gradual increase in their ability to resist hypoxia was noted. A study of the rate of change in resistance time was conducted on a sample of fry transferred from water containing 7.10 mg.O_2/l. to water containing 3.80 mg.O_2/l. The fish had been maintained in the bath containing 7.10 mg.O_2/l. for a month prior to the transfer. Immediately before the transfer, and at intervals during the period of maintenance at the lower level of oxygen, samples of fish were removed and experiments performed to determine their resistance times at a single lethal oxygen level (1.06 mg.O_2/l.). The results showed that the median resistance time increased progressively until an acclimation exposure time of about 110 hours (about 4½ days) had been reached. At this time a levelling of resistance times was observed. This change in median resistance time is illustrated in Figure 11. The data are summarized in Table VII. Statistically, the change in resistance time brought about by acclimation was highly significant. Thus, a decrease in the oxygen concentration of the environment is attended by a gradual change in the ability of the speckled trout to resist low oxygen.

A similar series of experiments was conducted on slightly older fry transferred from water containing 10.50 mg.O_2/l. to water with 3.94 mg.O_2/l., i.e., approximately twice the change in the experiment reported above. In these

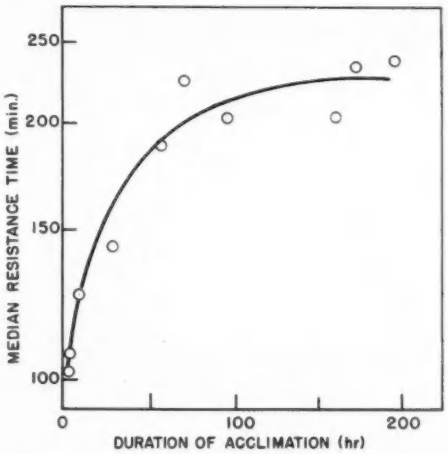

FIGURE 11. Changes in median resistance time accompanying acclimation of fry from 7.10 to 3.80 mg.O_2/l. Lethal level 1.06 mg.O_2/l.

experiments two different groups of fish were used; after transfer the first group was exposed to ordinary room lighting conditions 24 hours a day, while the second group was kept in complete darkness except for a short feeding period every other day. Owing to the stimulating effect of light and movements of the investigator, the fish tested in the light tended to be somewhat more active than those held in the dark. The results showed that fish transferred from 10.50 to 3.93 mg.O_2/l., and exposed to room lighting, approached complete acclimation by about 185 hours (approximately 7½ days) while fish maintained during the acclimation period in darkness, tended to take longer, completing their acclimation in about 235 hours (about 10 days). In this experiment the median resistance times were determined at a lethal oxygen level of 0.95 mg.O_2/l. The data are illustrated in Figure 12 and are summarized in Tables VIII and IX. As in the previous experiment, there were highly significant differences between the results of experiments conducted prior to transfer and after the apparent completion of acclimation. The differences in median resistance times for fish acclimated in the light and in the dark, when compared at similar acclimation durations, were not significant at the beginning and end of the experiment, although there was a marginal difference when acclimation was about half completed (at 117½ hours). The fact that the points for the dark-adjusted fish were consistently below those for the light-adjusted fish suggests that the more protracted acclimation of the dark-tested fish is a real trend, although, as indicated by the statistical comparisons, the effect is not of great magnitude.

Experiments on the rate of loss of low-oxygen acclimation were also conducted. Fingerling trout acclimated to 2.46 mg.O_2/l. were transferred to water

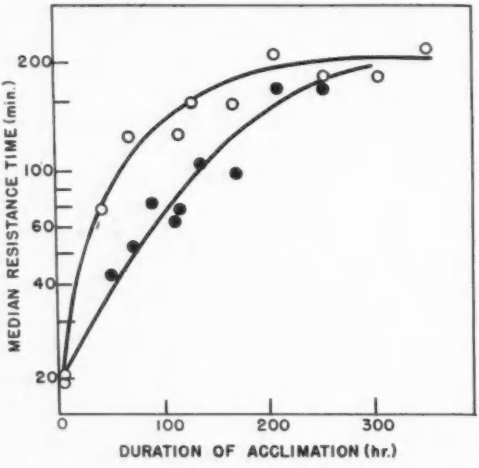

FIGURE 12. Changes in median resistance time accompanying acclimation of fry from 10.50 to 3.93 mg.O_2/l. Lethal level 0.95 mg.O_2/l. *Open circle*, fish acclimating in light; *solid circle*, fish acclimating in the dark.

containing 10.00 mg.O_2/l. After transfer the median resistance times of the fish decreased (Figure 13, and Table X). "Deacclimation" from the low to the high oxygen level seemed to be about 95% completed by about 150 hours (5 days). Thus, the increased resistance gained when fish are exposed to low-oxygen water is lost when they are returned to water containing higher concentrations of oxygen.

Data on the rate of acclimation are listed in the folowing table.

Acclimation range	*Difference*	*Time to 95% acclimation*	*Rates of acclimation*
(*mg.* O_2/*l.*)	(*mg.* O_2/*l.*)	(*hours*)	(*mg.* O_2/*l.*/100 *hr.*)
10.50 to 3.93 (in light)	6.57	187	3.50
10.50 to 3.93 (in dark)	6.57	235	2.80
7.10 to 3.80	3.30	109	3.01
2.46 to 10.00	7.54	152	4.95

In general, the rate of change of resistance accompanying acclimation varied between approximately 3 and 5 mg.O_2/l./100 hours of exposure; that is, in order to obtain 95% acclimation to a change of 1 mg.O_2/l. in the environmental oxygen concentration, from 20 to 33 hours of exposure were required. By doubling the exposure, one could be fairly certain of attaining almost complete acclimation of the animals. Thus, a tentative rule of thumb for acclimating young trout to low-oxygen conditions (at about 9°C.) would be: for each change of 1.0 mg.O_2/l. in environmental oxygen pressure, 70 hours is required for acclimation to approach completion.

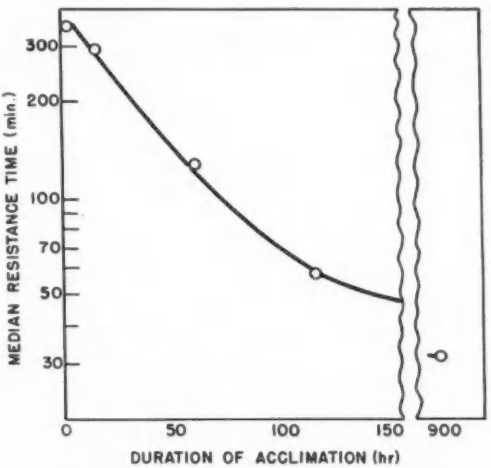

FIGURE 13. Changes in median resistance time accompanying acclimation of fry from 2.46 to 10.00 mg.O_2/l. Lethal level 1.07 mg.O_2/l.

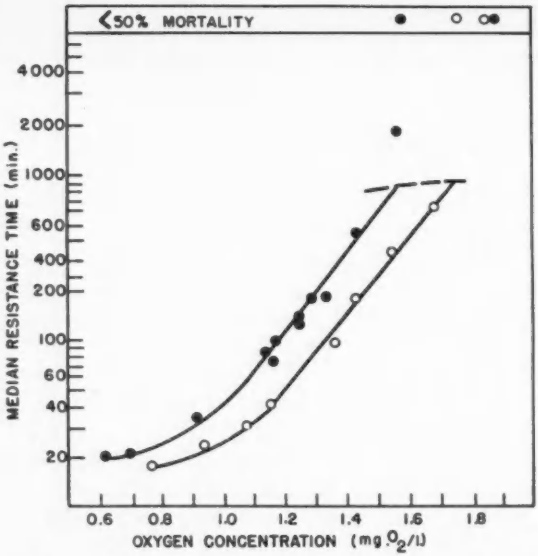

FIGURE 14. Median resistance times at various lethal oxygen levels for fry acclimated to two different oxygen concentrations. *Open circle*, acclimated to 10.50 mg.O_2/l.; *solid circle*, acclimated to 7.11 mg.O_2/l.

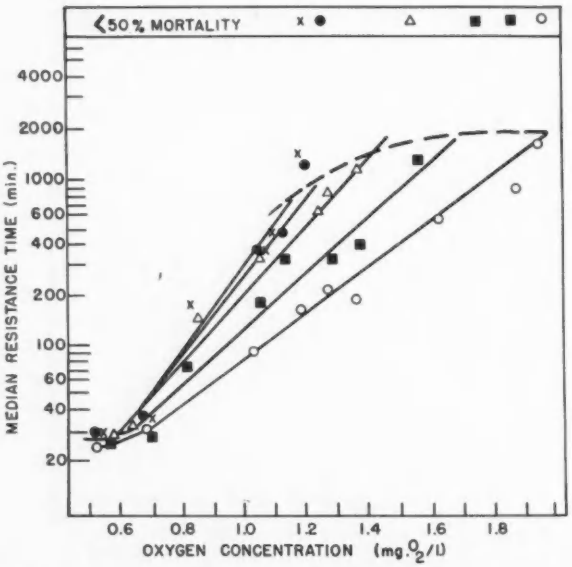

FIGURE 15. Median resistance times at various lethal oxygen levels of small fingerlings acclimated to five different oxygen concentrations. *Open circle*, acclimated to 9.30 mg.O_2/l.; *solid square*, acclimated to 7.14 mg.O_2/l.; *open triangle*, acclimated to 6.22 mg.O_2/l.; *solid circle*, acclimated to 4.56 mg.O_2/l.; *cross*, acclimated to 3.46 mg.O_2/l.

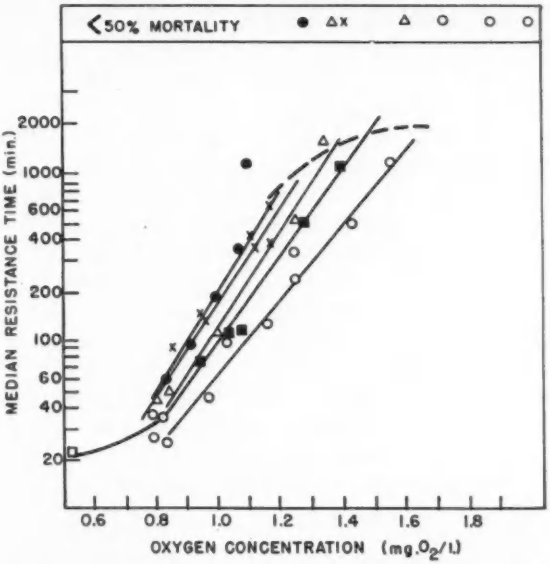

FIGURE 16. Median resistance times at various lethal oxygen levels of large fingerlings acclimated to five different oxygen concentrations. *Open circle*, acclimated to 10.70 mg.O_2/l.; *solid square*, acclimated to 9.15 mg.O_2/l.; *open triangle*, acclimated to 5.16 mg.O_2/l.; *solid circle*, acclimated to 3.59 mg.O_2/l.; *cross*, acclimated to 2.52 mg.O_2/l.

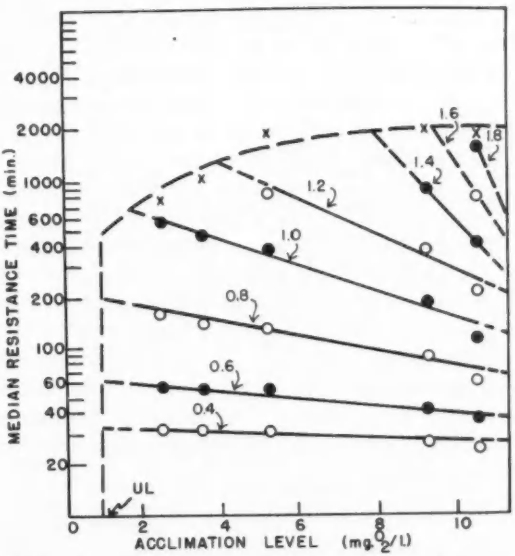

FIGURE 17. Relation of median resistance times at constant lethal oxygen levels to acclimation level. Figures in body of graph indicate lethal oxygen levels. Dotted line at top of graph relates the median times to death at the incipient lethal level with acclimation level. The oxygen concentration designated UL is the ultimate incipient lethal level.

(ii) EFFECTS OF ACCLIMATION ON RESISTANCE TIMES

The increase in resistance accompanying acclimation occurred at all lethal levels above that at which the resistance time approached a minimum. The median resistance times of fry acclimated to 7.11 mg.O_2/l. were between 1½ and 2½ times greater than those determined for fish acclimated to 10.50 mg.O_2/l. In Figure 14, the median resistance times obtained for fry acclimated to 10.50 mg.O_2/l. and 7.11 mg.O_2/l. are compared. Experiments performed on 5-month-old and 10- to 11-month-old fish confirm the view that acclimation is accompanied by a general increase in resistance times. In Figures 15 and 16 median resistance times of older fish acclimated to different levels are plotted. The data are summarized in Tables XI to XXII. Statistical comparisons showed that there were highly significant differences between median resistance times, determined at a given lethal oxygen concentration, for fish acclimated to different oxygen levels.

As suggested above, acclimation from high to low oxygen concentrations did not seem to involve an increase in the minimum resistance time of the fish. As shown in Figures 14 and 16, the minimum resistance times were about 27 minutes for 10- to 11-month-old fingerlings and about 19 minutes for the fry. The experiments on 5-month-old fish were performed when the design of the apparatus had not been developed sufficiently to determine resistance times at levels close to the asymptotic point. Examination of the available data indicates that the range of oxygen concentrations at which the minimum median resistance times were reached for different acclimation levels was quite narrow, lying between 0.50 and 0.60 mg.O_2/l. for the 10- to 11-month fish.

As demonstrated in Figure 16, the effect of acclimation on resistance is greatest at higher lethal levels. At low pressures (e.g., at 0.5 mg.O_2/l.), acclimation did not enhance the ability of fish to resist hypoxia detectably. This pattern is reflected in the slopes of the trend lines relating median resistance times and lethal oxygen levels for fish acclimated at different levels. In general, the higher the acclimation level, the smaller the slope of the trend line tended to be (see Table XXIII). The trend lines therefore tended to converge at pressures where the median resistance times were approaching a minimum (Fig. 16).

At any given lethal oxygen level, the logarithms of the median resistance times, for fish acclimated to different oxygen concentrations, have a roughly linear relation to the acclimation level (Fig. 17). As anticipated from examination of the data on the regression of resistance times on lethal oxygen level presented earlier, the slopes of the lines relating log resistance times with acclimation levels increased as the lethal oxygen level increased. As the acclimation level dropped, the maximum observed resistance times also dropped. Thus in the lower acclimation range when the effect of low oxygen pressure became lethal, mortality occurred relatively rapidly whereas in the higher acclimation range lethal effects were considerably protracted.

(iii) EFFECT OF ACCLIMATION ON INCIPIENT LETHAL LEVELS

Acclimation to low oxygen was accompanied by changes in incipient lethal levels, as well as by alterations in resistance times; fish acclimated to high oxygen levels had higher incipient lethal levels than those acclimated to lower acclima-

tion levels. In Figures 14, 15 and 16 the upper limit of each resistance line indicates the position of the incipient lethal level; the dotted line joins adjacent incipient levels. The relation between incipient lethal levels and acclimation oxygen levels appears to be one of simple direct proportionality; if the incipient lethal levels are plotted against acclimation oxygen levels, the data are well fitted by a straight line (Figure 18A). The data are summarized in Table XXIV. Statistical comparisons showed that incipient lethal levels at high oxygen levels were significantly different from those determined at low acclimation concentrations. The effect was uniform for all age groups studied, and thus the data for all experiments illustrated in Figures 14–16 were grouped for presentation in Figure 18A.

In the case of speckled trout under one year of age (at a temperature of 9°C.), the relation between acclimation and incipient lethal levels (Figure 18A) is illustrated by the following formula:

$$I = 0.87 + 0.086\,A \quad \ldots\ldots (2)$$

where A = acclimation level (mg. O_2/l.)
I = incipient lethal (mg. O_2/l.).

The ultimate incipient lethal level theoretically represents the lowest point to which fish can be acclimated without suffering more than 50% mortality. This level may be determined from equation (2) by solving for the values of I and A that satisfy the expression I = A. In this case the ultimate incipient lethal oxygen level was calculated to be 0.96 mg.O_2/l.

While statistics describing 50% mortality are of interest as comparative measures, the oxygen levels resulting in almost complete mortality, and those

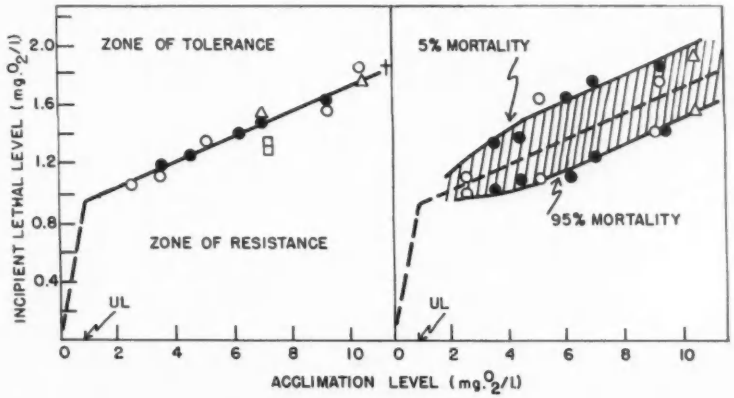

FIGURE 18. Incipient lethal levels for young speckled trout acclimated to different oxygen concentrations. A, Graph of 50% levels; B, Graph of 5% and 95% levels; UL, ultimate incipient lethal level; *open triangle*, experiments on fry (Series E); *solid circle*, experiments on small fingerlings (Series A and G); *open circle*, experiments on large fingerlings (Series C); *open square*, experiments on large fingerlings conducted at night (Series B); *cross*, experiments on yearlings (data from Graham, 1949).

which permit almost complete survival, are of more practical interest. Calculation of 5% and 95% lethal levels gives a picture of the range of incomplete lethal effects bridging the gap between survival and death in the population. The 95% and 5% incipient lethal levels did not bear the same direct proportional relation to the acclimation level observed for the 50% incipient level in Figure 18A. Instead, down to about 6 mg.O_2/l., the 5% and 95% incipient levels were uniformly and widely separated, while at lower levels the interval between the limits decreased so that at the lowest acclimation level recorded the two were almost equal (Fig. 18B). This indicates that the variability of response at the high acclimation levels was greater than at lower levels. The positions of the 5% and 95% lines delimit the general tolerance and resistance limits of the group of fish studied. At oxygen levels (on the Y axis) above the 95% line almost all the fish survived the primary effects of low-oxygen stress ("zone of tolerance"). Below the 5% line almost all the fish died from oxygen lack ("zone of resistance"). Between the two lines, varying percentages of mortality occurred, 50% mortality roughly bisecting the zone (intermediate zone cross-hatched in Fig. 18B).

Thus, acclimation to low but not lethal oxygen levels was accompanied by an increase in the ability of young speckled trout to tolerate low environmental oxygen concentrations.

Effects of Growth on Resistance and Tolerance

During their first year of life, tolerance of speckled trout to low-oxygen conditions did not change detectably (see Fig. 18). However, during this period

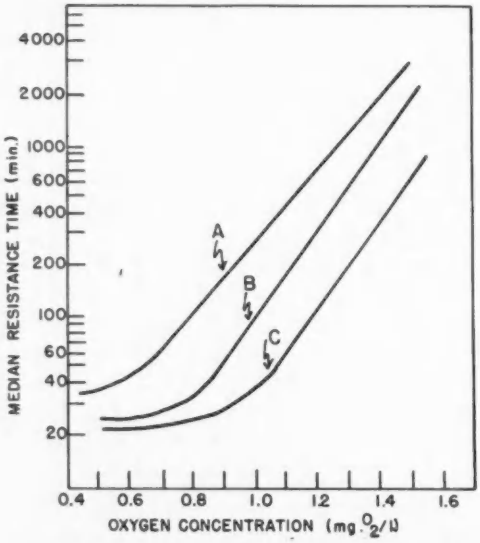

Figure 19. Trend lines relating median resistance times at various lethal levels for fish of three different sizes all acclimated to approximately 7.10 mg.O_2/l. A, large fingerlings (9.9 cm., 12.1 g.)—data obtained by interpolation from Figure 17; B, small fingerlings (6.8 cm., 3.8 g.)—data obtained from Figure 15; C, fry (4.3 cm., 0.92 g.)—data obtained from Figure 14.

striking changes occurred in the resistance of the fish. The data indicate that smaller fish tended to be less resistant to oxygen lack than larger ones. As an illustration of the effects of age on resistance, the relative resistance of 2-month-old fry, 5-month-old fingerlings and 10- to 11-month-old fingerlings acclimated at 7.10 mg.O_2/l. are compared in Figure 19. The curve for 10- to 11-month-old fingerlings was obtained by interpolation from Figure 17. Thus for fish under one year of age, the older fish tended to be more resistant, but no more tolerant, to oxygen lack than younger, smaller fish.

Effects of External Stimuli on Resistance and Tolerance

Comparisons of the relative resistances of trout fingerlings tested in complete darkness and those tested under 24-hour stimulation from room lighting, show that the dark-tested fish tended to be more resistant to lethal oxygen conditions than their light-tested counterparts (Fig. 20). This difference can probably be attributed to the fact that fish tested in the light have a higher metabolic demand for oxygen than fish tested in the dark, remote from most external stimuli.

Difference in the duration of the pre-exposure period did not influence the time to death to any extent. Of the two groups of fish tested in the light, one

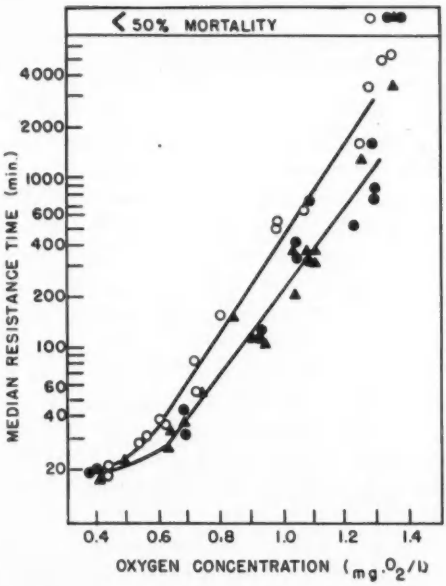

Figure 20. Median resistance times at various lethal oxygen concentrations for large fingerlings. Tests conducted under different conditions. *Open circle*, fish held in experimental flasks 24 hours before introduction of low-oxygen water. Tests conducted in the dark; *solid circle*, fish held in experimental flasks 24 hours before introduction of low-oxygen water. Tests conducted in the light; *closed triangle*, fish held in experimental flasks 30 minutes before introduction of low-oxygen water. Tests conducted in the light.

group was placed in the flasks 24 hours before the introduction of water low in oxygen, the other, just 30 minutes before the imposition of lethal conditions. There was no detectable difference in resistance between these two groups, indicating that the pre-exposure duration had no appreciable influence on the resistance patterns of the fish. The results of these experiments are also illustrated in Figure 20 and summarized in Tables XXV–XXVII.

The incipient lethal levels for these experiments were lower than would be expected from an examination of incipient lethal levels obtained in experiments concerned with the effects of acclimation (see Fig. 18). In the series of experiments on the effects of external factors the incipient lethal level was 1.34 mg.O_2/l. By interpolation the incipient level for the fish tested in the previous experiments acclimated to 6.80 mg.O_2/l. would be about 1.44 mg.O_2/l. A contributing reason for this difference may be that experiments designed to test the effects of external factors were begun at midnight, when the metabolic rate tends to be low (Graham, 1949). A low metabolic demand for oxygen at this time might tend to reduce the oxygen level necessary for the maintenance of life.

The conduct of experiments in the light rather than in the more uniform conditions of darkness did not appreciably affect the variability within experiments. Comparisons of the slope functions at comparable lethal levels for the three series of experiments, Table XXVIII), indicated that the variability within the experiments was very similar regardless of experimental conditions.

EFFECT OF ACCLIMATION ON OXYGEN-DEPENDENT RESPIRATION

To investigate one of the physiological factors underlying acclimation, the oxygen uptake of young trout in low-oxygen environments was studied. Three series of experiments were conducted to determine the active metabolic rates of fry, fingerlings and yearlings when the animals were exposed to low (but not lethal) levels of oxygen. In each series of experiments the metabolic rates of two groups of fish acclimated to two different oxygen levels were compared.

In experiments on yearling fish (av. wt. 24.9 g.), using the methods of Fry and Hart (1948), there was a tendency for fish acclimated to a low oxygen concentration (3.5 mg.O_2/l.) to remove more oxygen than fish acclimated to a higher level (7.0 mg.O_2/l.). However, since the variations within individual experiments were quite wide, the differences noted could not be considered significant. The results of four experiments are illustrated in Figure 21C.

Experiments of fingerlings (15.6 g.) and fry (2.20 g.), with better controlled experimental conditions (see p. 398), demonstrated conclusively that, at oxygen levels in the zone of respiratory dependence, fish acclimated to a low oxygen level remove oxygen at a greater rate than fish acclimated to a higher oxygen concentration. The results of the experiments on fish of the two size groups are shown in Figures 21A and B. Below about 4.0 mg.O_2/l. the advantage in uptake rate gained by fish acclimated to low oxygen pressures over those acclimated at higher levels decreased as the environmental oxygen pressure dropped. No difference between the rates of uptake above about 5.0 mg.O_2/l. (slightly less than half of air saturation) could be detected.

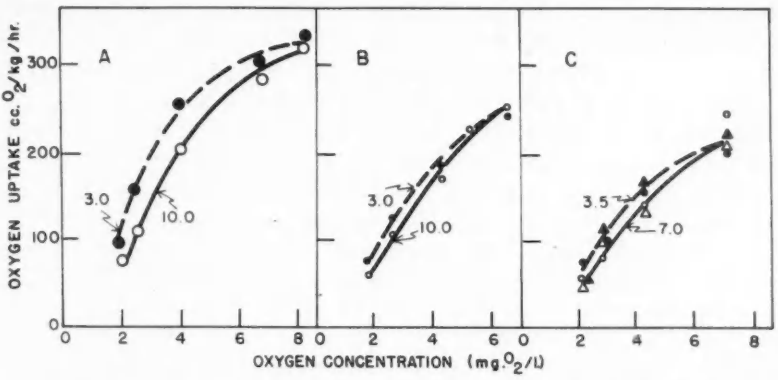

FIGURE 21. Oxygen uptake at various environmental oxygen concentrations in young speckled trout acclimated to different oxygen concentrations. Acclimation levels in mg.O_2/l. indicated by figures in body of graph. A, fry, 2.2 g.; B, fingerlings, 15.6 g.; C, yearlings, 24.9 g.

In the zone of dependence the relation between uptake and pressure was curvilinear, the rate of oxygen uptake decreasing at a progressively greater rate as the environmental oxygen pressure dropped. This finding does not agree with Graham's (1949) interpretation that the oxygen dependent respiration of yearling speckled trout bears a direct linear relation to oxygen pressures below the

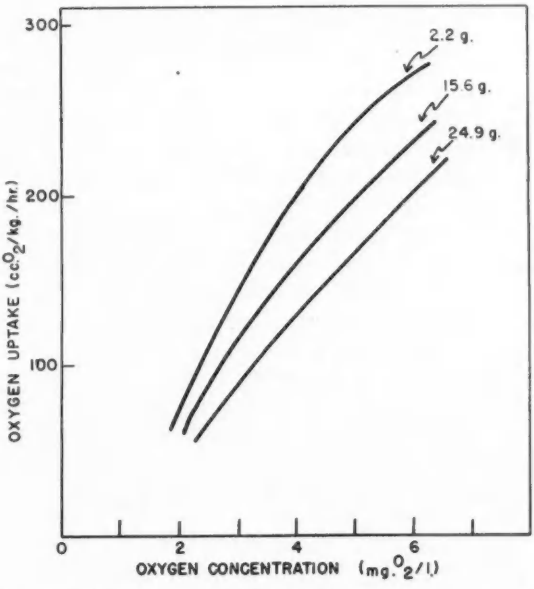

FIGURE 22. Oxygen uptake of young speckled trout of different sizes acclimated to oxygen concentrations between 7.0 and 10.0 mg.O_2/l. Average weights of fish indicated by figures in body of graph.

incipient limiting level. However, in their general shape the curves closely resemble those determined by Job (1955) for speckled trout of various sizes. Comparisons between the oxygen-dependent rates of uptake of the three different age groups indicate that the fry maintained a higher rate of oxygen consumption per unit weight than did either of the other groups. In turn, at the same oxygen levels the fingerlings removed proportionately more oxygen than did the yearlings. These findings are illustrated in Figure 22 where comparisons are made of the oxygen-dependent uptake rates of fish of the three size groups.

Analyses of variance were performed on the results of the experiments conducted on fry and on the fingerlings to demonstrate the effects of acclimation and of size differences on the rate of oxygen uptake. In the following table the results of the analyses are summarized. Where significant differences in uptake were noted, the degree of significance (expressed as the probabilities of such differences occurring by chance) is listed in the table.

		Main effects			*Interactions*		
Test level ($mg.\ O_2/l.$)		*Acclimations*	*Sizes*	*Runs*	AXS	AXR	RXS
Fry	2.00	$<.01$	.05	..	..	..	..
	2.54	$<.01$	$<.01$	..	..	..	..
	3.88	$<.01$	..	$<.01$	..	..	..
	6.88	..	..	..	..	..	..
	8.50	..	..	..	..	..	..
Fingerlings	1.80	.02	$<.01$	..	.05	..	..
	2.82	$<.01$	$<.01$	..	..	.05	..
	4.55	$<.01$	$<.01$	..	..	..	..
	6.72	..	.01	..	..	..	..

Examination of the table shows that at lower environmental oxygen levels there were highly significant differences between the rates of oxygen uptake of fish acclimated at different oxygen levels. In every experiment performed on fingerling trout, there were highly significant differences between the rates of oxygen uptake of fish of different sizes. This corroborates the conclusions drawn from comparisons of the oxygen consumption rate curves in Figure 22, that the larger fish did not take up oxygen at as rapid a rate per unit weight as smaller fish. In two out of the five experiments conducted on fry, the same type of difference was detected. However, as the fry tended to be of a more uniform weight than the fingerlings, the same clear-cut size effect demonstrated in the fingerling experiments could not be expected. In only one experiment was there a significant difference between the rate of oxygen uptake determined in replicate experiments. No concrete reasons for this difference could be determined from the data. Two interaction components showed significant differences at the 95% confidence level.

DISCUSSION

Resistance and Lethal Oxygen Level

The relation between time to death and lethal oxygen level in fish has been considered in two papers; Graham (1949) reported some preliminary experiments

on speckled trout yearlings, while Herbert and Merkens (1952) presented data on the relative resistance of rainbow trout to hypoxia. The interpretations of these authors differs from those presented in the present paper.

On the basis of preliminary experiments, Graham suggested that an hyperbolic relationship existed between resistance time and oxygen level. As suggested by her interpretation, this relationship might be represented as:

$$T_{50}\,X = K \quad \ldots\ldots (3)$$

where X = lethal oxygen level
T_{50} = median resistance time
K = a constant.

Herbert and Merkens (1952) suggested that resistance data for rainbow trout were adequately described by a formula similar to:

$$X^{a'}/T_{50} = b' \quad \ldots\ldots (4)$$

where X = lethal oxygen level
T_{50} = median resistance time
a' and b' = constants.

It will be recalled that, in the present paper, data on resistance at different lethal oxygen levels followed an exponential pattern. This can be described by the general equation:

$$T_{50} - t = ae^{bX} \quad \ldots\ldots (5)$$

where X = lethal oxygen level
T_{50} = median resistance time
t = minimum resistance time
e = 2.71828
a and b = constants.

This relationship was valid over the whole range of lethal oxygen levels from that at which the median resistance times approached a minimum value up to the incipient lethal level.

Re-examination of Graham's and Herbert and Merken's data suggests that the semi-logarithmic plot outlined in the present paper may offer a better description of lethal oxygen data for fish than either of the other two suggested formulations. Their data are illustrated in Figure 23 along with values obtained by the author on speckled trout fry. In each case, the data are plotted in three ways: as untransformed data on arithmetic axes, as data transformed according to the interpretation of each author and finally as a semi-logarithmic plot from which the "minimum time to death" was subtracted from each median resistance time. There is an apparent similarity in the general shape of the curves describing the untransformed data. The double-log plot of Herbert and Merken's data (based on the equation $X^{a'}T_{50} = b'$ which they proposed) results in a curve, whereas the data are well fitted by a straight line on the modified semi-log plot. Graham's sparse data, derived from experiments involving single fish only, are fitted by approximate straight lines on both the semi-reciprocal plot (based on the equation $T_{50}X = K$) and on the modified semi-logarithmic plot. Her data are

too few to draw any final conclusions on the form of the curve. Both the exponential and hyperbolic formulations fit the limited data with about equal precision. The author's data are included in Figure 23 to illustrate again the relatively close fit obtained by plotting the logs of adjusted resistance times against oxygen level.

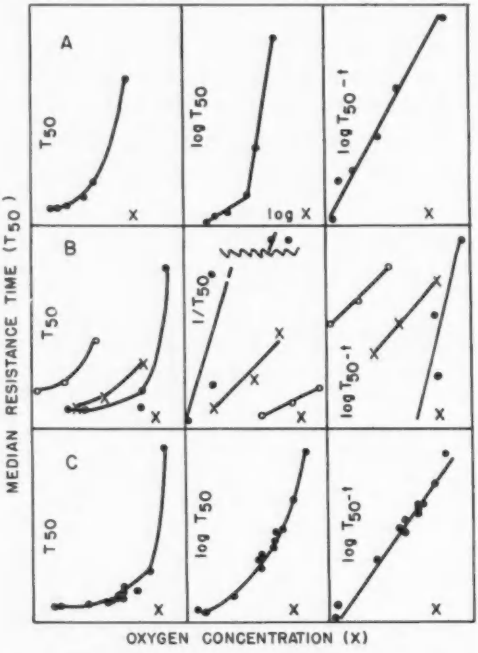

FIGURE 23. Median resistance times at various lethal oxygen levels in two salmonids. See text for explanation of transformations. *Row A*, data on rainbow trout from Herbert and Merkens, 1952; *row B*, data on yearling speckled trout from Graham, 1949; *row C*, data on speckled trout fry, acclimated to 7.11 mg.O_2/l., collected by the author.

As a further means of assessing the relative suitability of the three suggested relationships, attempts were made to fit a more extensive series of the author's data by hyperbolic and power curves as well as by the modified exponential configuration. Data from three typical experimental series were selected from experiments on fry and small and large fingerlings. Semi-reciprocal and double-logarithmic plots and semi-logarithmic plots in which the "minimum time to death" was subtracted were drawn up. The results are illustrated in Figure 24.

The semi-reciprocal plot resulted in a definite curve in all cases. It is evident that if "minimum times to death" were subtracted from the median resistance times, the amount of curvature would be increased (i.e. reciprocals of resistance times for lower oxygen levels would become relatively greater than those for

higher levels). Thus the hyperbolic formulation does not accurately describe low-oxygen resistance data for young trout.

The double-log plot does not produce a straight-line relationship. If the "minimum times to death" are subtracted, the fit is improved, but a marked curvature still persists.

The points on the modified semi-logarithmic plots are well fitted by straight lines. However, in experiments on large fingerlings (i.e. column C, Fig. 24) subtraction of the minimum time to death results in median resistance times at low oxygen levels tending to fall below the trend line. The discrepancy is not great.

In general, the relation between median resistance times and lethal oxygen level is best approximated by equation (5). Thus, above a critical level, for a unit increase in lethal oxygen level, an exponential increase in resistance time occurs.

The flexure at the lower end of the resistance lines is probably associated with changes in the efficiency of the gas transport mechanism. In theory, the relation between oxygen uptake and environmental oxygen concentration in simple forms follows an hyperbolic pattern, with the origin of the curve relating uptake to concentration having its origin at zero (e.g. Tang, 1933; Shoup, 1930). The possession of complex respiratory and circulatory systems by higher forms

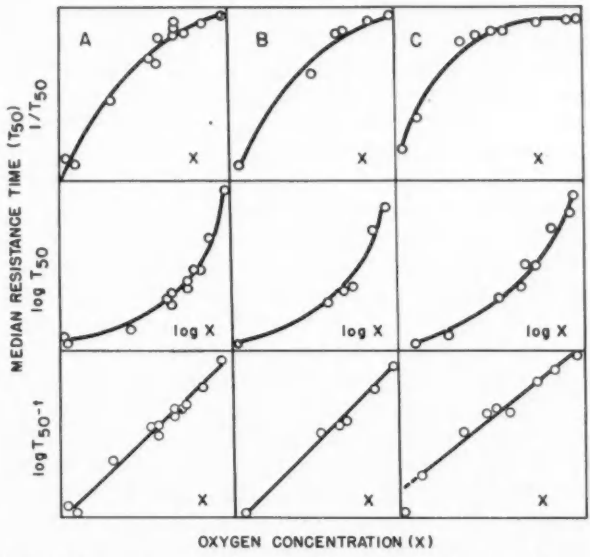

FIGURE 24. Median resistance times at various lethal oxygen levels for young speckled trout. *Upper row* of curves, semi-reciprocal plots; *middle row*, double logarithmic plots; *lower row*, modified semi-logarithmic plots. *Column A*, fry acclimated to 7.11 mg.O_2/l.; *column B*, small fingerlings acclimated to 7.14 mg.O_2/l.; *column C*, large fingerlings acclimated to 10.70 mg.O_2/l.

undoubtedly modifies this pattern. If the uptake curves for speckled trout (at approximately 10°C.) obtained by the author (Fig. 21, 22), by Graham (1949) and by Job (1955) are extrapolated, they cut the environmental oxygen concentration axis at a point above zero (at about 1 mg.O_2/l.). As illustrated in Figures 14, 15 and 16, between 0.7 and 1.0 mg.O_2/l. the resistance times of young speckled trout approach a constant minimum value. These data suggest that just below 1.0 mg.O_2/l. the oxygen uptake of the fish is for practical purposes reduced to zero and that, because of this, further reduction of environmental oxygen pressure does not speed mortality appreciably.

In theory the oxygen uptake curve would not be sharply terminated at 0.7 to 1.0 mg.O_2/l.; diffusion of gas to the living tissues of the animal would continue even if circulation ceased, and thus the uptake curve would be characterized by a sharp flexure at its lower end and would have its origin at zero. E. C. Black (unpublished data) found that at a temperature of between 9.5° and 11.0°C. trout in sealed bottles could remove oxygen from the water down to a pressure of about 0.7 mg.O_2/l. Wiebe *et al.* (1934) conducted experiments on sticklebacks similar to those of Black. They found that when the pH of the water in the flasks was near neutrality, the residual level was very close to the critical pressure where the fish could no longer remove significant amounts of oxygen from the medium; if after asphyxiation the fish in the flask was replaced by another, the second fish died very rapidly without having extracted an appreciable quantity of oxygen from the water. In view of Wiebe's results, the figure obtained by Black probably approximates the point where the oxygen uptake of the trout approaches zero. Black's value is very close to the concentration at which resistance times in young trout approach a minimum value.

The apparent inability of the circulatory system to supply oxygen to the cells at this critical level cannot be due to a breakdown of transport of oxygen from the blood to the cells. Ferguson and Black (1941) showed that the oxygen pressure of venous blood in active trout is almost zero. Thus, if any oxygen was carried in the blood, it would probably be rapidly removed by the tissues. There are two other factors that could readily account for the breakdown of transport at low oxygen pressures. The gradient of oxygen pressure between the environment and the blood may not be sufficient to effect transfer of any oxygen to the haemoglobin. Data derived from the work of Irving *et al.* (1941), on the oxygen dissociation properties of trout blood, indicate that at pressures between 0.5 and 0.7 mg.O_2/l. (at 10°C.) the blood could be only 20% to 30% saturated with oxygen at a maximum. From about 0.8 to 0.4 mg.O_2/l. the percentage saturation of the blood drops from 50% to 10%. Thus, in the range of concentrations where the efficiency of the blood for oxygen transport is rapidly decreasing, oxygen uptake is approaching zero.

The second factor contributing to the breakdown of respiration is the apparent susceptibility of the central nervous system. At a critical low oxygen pressure, the integrating mechanism controlling respiration abruptly ceases to function. When this occurs, ventilation rapidly ceases and the possibility of removing oxygen from the environment is even further reduced. Observations

indicate that this collapse occurs at pressures in the region of the residual level. At those levels, even though spasmodic movements take place for a considerable time, regular respiratory movements are soon abolished after the initial exposure. In general, the curve relating oxygen uptake and environmental oxygen pressure in young speckled trout is probably sigmoid in shape. The flexure at lower pressures is probably associated with a decrease in the ability of the blood to take up oxygen through the gills and with failure of the coordinating mechanism controlling respiratory movements. At the point of flexure the rate of oxygen uptake would be almost zero.

Effects of Acclimation on Resistance, Tolerance and Oxygen Uptake

Acclimation to low oxygen was manifested by an increased resistance and tolerance to hypoxia and by an apparent increase in the ability of the fish to extract oxygen from the environment at low pressures. As indicated by changes in resistance, the acclimative change comes about slowly, suggesting that the process involves deep-seated physiological changes.

In mammals, acclimation to low oxygen pressures is attained largely through increases in the efficiency of the gas transport mechanism; i.e., by adjustments in blood chemistry, and increase in the haemoglobin content of the blood through hemopoeisis (see Van Liere's review, 1943). These changes result in an increase in the percentage volume of oxygen in the blood leaving the alveoli, which permits the animal to maintain a higher rate of oxygen supply to the cells than if acclimation had not occurred. As indicated by the increase in oxygen uptake at low pressure (see Fig. 21), adjustments in the transport system similar to those observed in mammals probably occur when young speckled trout acclimate to low oxygen levels.

Information obtained in lethal oxygen experiments also suggests that low-oxygen acclimation in young trout primarily involves changes in the oxygen capacity of the blood. Examination of Figure 16 indicates that the resistance lines tended to converge at low pressures, so that the oxygen pressure at which resistance times approach a minimum value is not detectably changed by acclimation. As suggested earlier, this "residual level" represents the point where the haemoglobin of the blood is no longer an efficient oxygen carrier. At this level, the factor limiting respiration is the oxygen pressure of the blood *per se*, and not the absolute quantity of oxygen present. If acclimation involves an increase in capacity primarily, there would be no effect at pressures below the residual level. At pressures above this, the amount of metabolism that could be carried out would tend to be dependent on the quantity of oxygen in the blood. Thus, the increase in capacity would permit more oxygen uptake and extend the resistance times of fish at oxygen concentrations nearer the incipient lethal level. The experiments on resistance of young trout confirm this suggestion; the effects of acclimation on resistance times are least at low levels and greatest at levels in the upper part of the zone of resistance. Thus acclimation apparently involves a change in the oxygen capacity of the blood rather than a change in pressures at which oxygen can be loaded and unloaded by the blood (i.e., a change in the

affinity of the blood for oxygen). Direct experimentation is needed to confirm this indirect evidence.

Effects of Size on Resistance, Tolerance and Oxygen Uptake

At the incipient lethal level the transport mechanism operating at maximum capacity can just supply the minimum demands of the animal for oxygen. Experiments showed that in speckled trout tolerance did not change appreciably during the first year of life; incipient lethal levels for fry and large fingerlings were not detectably different. Despite this fact, the maximum rate of oxygen uptake per unit weight tended to drop with increase in size (Fig. 22). Job's (1955) findings on maximum and standard rates of uptake in trout of different sizes, offer a reasonable explanation for this observation. He found that at 10°C. both the maximum and standard metabolic rates of uptake at low oxygen levels increased at approximately the same rate as the fish grew larger; for a unit decrease in demand, the supply dropped a like amount. Thus, the pressure at which the minimum demands of the animal are just met by the supply would not change with growth. Job's data indicate that this relationship holds true only in the region of 10°C.

Wells (1913) and Keys (1931) found a positive relation between resistance and size in several species of fresh-water fish and in *Fundulus*. As indicated in Figure 19, the data on young speckled trout conform to this pattern. Without further experiments no complete explanation for this trend can be forwarded. Keys suggested that the decrease in resistance accompanying growth was associated with a decrease in the rate of oxygen uptake per unit weight. Martin (1941) noted that the ability of embryo speckled trout (as well as that of Atlantic salmon and killifish) to resist severe hypoxia decreased as development proceeded. She concluded that this change was due to an increasing subordination of the functions of the animal to the control of the central nervous system, which, presumably, is more susceptible to hypoxia than the other organ systems. To harmonize with results of experiments performed by the author, it is suggested that this increase in susceptibility must end shortly after hatching, and must be replaced by a trend in the opposite direction; owing to changes in metabolism, the resistance of older fish becomes greater than that of the young.

Changes in hormone balance accompanying development affect metabolism and would be expected to influence the resistance of fish. Experiments reported by Zaks and Zamkova (1952) indicate that inhibition of thyroid activity by thiourea results in a decrease of standard oxygen uptake at higher oxygen pressures, and apparently, an increased resistance to oxygen lack. An interesting feature of this work was that thiourea-treated fish were able to remove more oxygen at low pressures than untreated fish. Thus, there was not only a decrease in demand but also some change in the efficiency of gas exchange.

Keys (1931) noted a sexual difference in the resistance of *Fundulus* to hypoxia. Although the resistance of male and female fish tended to be the same throughout most of the year, during the breeding season male fish were more resistant than females.

Effects of Activity on Acclimation, Resistance and Tolerance

Experiments demonstrated that fish exposed to light during lethal experiments died more rapidly than fish tested in darkness (see Fig. 20). On the other hand, fish held in the light tended to become acclimated to low oxygen levels more rapidly than fish shielded from the light (Fig. 12). The effects are probably associated with the stimulating influence of light on the oxygen demand of the fish.

At levels where, even with a maximum effort, the fish is not able to supply its minimum needs for oxygen, the imposition of further demands would tend to hasten death. On exposure to very low lethal levels the fish respond violently, and very soon lose equilibrium. In the presence of the strong stimulus to activity supplied by the sudden imposition of severe oxygen lack, the stimulating effects of light would not be appreciable. Confirming this suggestion, at very low levels there was no difference in the times to death of fish tested in the light and in the dark. However, at levels nearer the incipient lethal level where the fish temporarily regain equilibrium after the initial exposure, stimulation by light apparently raised the oxygen demand sufficiently to speed mortality.

Stimulation by light tended to speed the acclimation of the fish to low oxygen. In the zone of respiratory dependence, the maximum rate of oxygen uptake is restricted by the oxygen pressure of the environment. However, if the animal is quiescent its demand for oxygen can be supplied readily without the respiratory system working to its maximum capacity. Acclimation would not be expected to occur unless the animal was sufficiently active to suffer a limitation of oxygen uptake. Fry (1947) has summarized this view as follows: Before acclimation to a limiting factor (such as oxygen pressure) occurs "some stress is exerted on the organism which is the stimulus that brings out the adaptive response. . . . When a limiting factor is operating, the stress is imposed by the organism itself, for if the organism remained completely quiescent it would not be affected by the factor in question". If restriction of metabolism is the stimulus for acclimation, then those fish exposed to the light, tending to be more active, would be subject to more intense stimulation than the quiescent fish in the dark. This effect apparently results in a more rapid, though no more extensive, acclimative adjustment in the light-tested fish.

Tolerance Measures and Ecology

Experimental procedures outlined in this paper provide a method for describing the low-oxygen tolerance limits of fish. In ecology, the need for precise measures of tolerance in studying the environmental relationships of fish has been emphasized repeatedly (e.g. discussion in Moore, 1942). In many situations, environmental oxygen pressure may influence the success of a species, either by exerting rapid lethal effects similar to those described in this paper, or by limiting the activity of the fish so that it cannot compete successfully or defend itself where better adapted species are present. In situations where oxygen depletion occurs, to understand the relation between the fish and its physical and

organic environment, laboratory experiments are needed to define precisely the capacity of the animal to withstand hypoxia.

Data on resistance and tolerance, similar to those presented in this paper, illustrate the capacities of fish to withstand the short-term effects of severe hypoxia, but will not account for results of prolonged exposure to pressures slightly above the incipient lethal level. Fish held at oxygen levels in this range were sluggish in their movements, fed poorly and were susceptible to disease. Under these conditions the animal is not well equipped to meet the attacks of better adapted predators, disease and deleterious effects of accessory factors in the physical environment. (For further discussion see Lindroth, 1948; Graham, 1949.)

In carrying out experiments on the short-term effect of oxygen lack, the various sources of variability outlined in this paper must be considered. At a given temperature, the acclimation history of the animal and variability in size may have important effects on the resistance patterns of the fish.

For a complete picture of the capacity of the animal to withstand hypoxia, descriptions of both resistance and tolerance are necessary. In some instances, where severe oxygen depletion is of short duration, the survival of the animal may depend on its ability to live for a limited period at oxygen levels where more prolonged exposure would result in mortality. In other cases, where the lowering of the environmental oxygen concentration is more gradual, short-term resistance would not help the fish to withstand the limiting conditions. Here the ability of the animal to lower its tolerance limits by acclimation would be the main factor in determining whether or not the fish could survive. As resistance and tolerance are not completely interdependent (e.g. experiments showed that growth is accompanied by an increase in resistance, but *not* in tolerance), inferences concerning the relative resistance of the species cannot be accurately drawn from knowledge of the tolerance limit alone.

Examples can be cited where the ability of fish to resist oxygen lack for short periods is important in determining the survival of a species. Severe oxygen depletion of short duration often occurs in small bodies of water where there is a heavy growth of aquatic vegetation. In warm weather, a nocturnal lowering of oxygen level may occur as a result of diurnal variations in plant metabolism (e.g. Broekhuysen, 1935). Short-term resistance to hypoxia apparently permits certain fish to make feeding forays into oxygen deficient waters. Field observations (e.g. Pearse and Achtenburg, 1920; Hile and Juday, 1941; and Sprugel, 1952) indicate that, during summer stratification in lakes, bluegills, lake trout and yellow perch may be captured in the deeper waters where the oxygen content of the water is low. Thus these fish, through their powers of resistance, can temporarily extend their range of habitation. This ability may be important for bottom-feeding fishes who would starve if they did not have access to benthic waters where the environmental oxygen pressure often drops to a low level.

Where oxygen depletion occurs more slowly, as, for instance, under ice cover in the winter (e.g. Greenbank, 1945), the ability of the animals to become acclimated to a gradual decline in oxygen supply is an important factor in deter-

mining whether or not the fish can exist in an area. Observations by Jahoda (1947), Nikiforof (1952), and Gutsell (1929), indicate that fish in stagnant water, where the environmental oxygen concentration is lowered by the fishes' respiration, can be acclimated to the limiting conditions and extend their tolerance limit downward. An important consequence of this acclimation is that at low oxygen pressures the animal's ability to supply oxygen to the cells increases, permitting it to maintain a wider scope for activity at low pressure than if the adjustment had not been made. This increased ability would undoubtedly aid the fish in capturing prey or escaping from predators and enhance its chances of surviving.

By studying resistance and tolerance of fish to oxygen lack, a better understanding of the role of oxygen in determining the success or failure of a species in a given body of water can be gained. It is hoped that this paper provides, in some measure, a method of attacking the problem in the laboratory, and that, by pointing out some of the factors influencing resistance and tolerance of fish to hypoxia, it defines the general problem more clearly.

SUMMARY

The ability of young speckled trout (*Salvelinus fontinalis*) to withstand oxygen lack has been investigated. The tolerance limits of the trout were determined by exposing samples of fish to a graded series of low oxygen concentrations and noting the level which just failed to cause 50% mortality (the incipient lethal level) within a period of 5,000 minutes. The times to death (resistance times) of individual fish were recorded. All experiments were performed at 9°–10°C.

BEHAVIOUR AND HYPOXIA. Exposure to low oxygen stimulated the fish to swim vigorously and to "surface". Loss of equilibrium followed this initial activity. At very low levels of oxygen, cessation of respiratory movements occurred shortly thereafter. At higher levels, the fish regained equilibrium. At concentrations below the tolerance limit, a secondary collapse followed by death occurred.

RESISTANCE AND OXYGEN LEVEL. Above a critical low oxygen level, resistance times increased exponentially with an increase in concentration. Below the critical level, resistance times tended to approach a constant, low value.

ACCLIMATION. Changes in environmental oxygen level (above the tolerance limit) were accompanied by a slow change in the resistance and tolerance of the trout. A drop in environmental pressure was accompanied by an increase in the ability of the fish to withstand oxygen lack. For a change of 1.0 mg.O_2/l. in environmental concentration from 20 to 33 hours passed before acclimation approached completion.

(*a*) Change in tolerance. For fish acclimated to air saturation, the incipient lethal level was about 1.85 mg.O_2/l. For a unit decrease in acclimation concentration, the tolerance limit dropped by 0.086 mg.O_2/l. The lowest concentration to which young speckled trout could be acclimated without significant mortality occurring was estimated to be 1.05 mg.O_2/l.

(*b*) Change in resistance. The effects of acclimation on resistance were

proportionately greater at levels near the tolerance limits than at very low concentrations. Acclimation did not enhance the ability of the fish to withstand almost total deprivation of oxygen. However, at medium lethal levels, up to five-fold increases in the time fish could withstand hypoxia occurred.

Acclimation to low oxygen was accompanied by an increase in the ability of the fish to remove oxygen at concentrations below about 4.0 mg.O_2/l.

SIZE. Increase in size from 0.96 to 12.1 g. was not attended by a change in tolerance. However, large fish tended to live longer at a given lethal level than the small fish. Growth was accompanied by a decrease in the maximum rate of oxygen uptake per unit body weight.

EXTERNAL STIMULI. Fish exposed to the light, and persumably having a higher oxygen demand, tended to be less resistant to hypoxia than fish tested in the dark. However, young trout tended to become acclimated to low levels of oxygen more rapidly when stimulated by light than when held in the dark.

THE RESISTANCE-OXYGEN LEVEL CURVE. The following empirical relationship was established:

$$T_{50} - t = ae^{bX}$$

where X = lethal oxygen level (mg. O_2/l.)
T_{50} = median resistance time (minutes)
t = minimum resistance time (minutes)
a, b = constants
e = 2.71828.

Data on the resistance of speckled and rainbow trout, collected by other workers, were fitted by this equation.

THE OXYGEN UPTAKE CURVE. In speckled trout, the curve relating rate of oxygen uptake and environmental oxygen pressure is probably sigmoid in shape. The flexure at low oxygen levels reflects the failure of the blood to extract oxygen from the environment. At the point of flexure, oxygen uptake probably approaches zero.

ACCLIMATION AND RESPIRATION. Data on resistance and oxygen uptake strongly suggest that acclimation to low oxygen is accompanied by an increase in the efficiency of the gas transport mechanism. An increase in the oxygen capacity of the blood, similar to that occurring in mammals, is likely.

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APPENDIX

Key x—a variable

s_x—standard deviation of x

$\bar{x}$—mean of x

$s_{\bar{x}}$—standard error

ET_{50}—median resistance time (see p. 401)

ED_{50}—incipient lethal oxygen level (see p. 402)

S—slope function (see p. 401)

O_2—oxygen concentration (mg.O_2/l.)

N—number of individuals

M—number of individuals dead

*—experiment terminated before 5,000 min.

a—intercept.

b—slope

TABLE I. Size of speckled trout used in experiments.

Stage	Experimental series	Date	N	Mean length $\pm s_x$	Mean weight $\pm s_x$
				cm.	*g.*
	D	April, '51	59	3.53 ± 0.06	— —
Fry	E	May, '51	56	4.30 ± 0.03	0.92 ± 0.03
	F	May, '51	97	4.30 ± 0.03	0.96 ± 0.02
Small fingerlings	G	July, '51	42	6.16 ± 0.07	2.27 ± 0.13
	A	Aug., '50	116	6.80 ± 0.07	3.78 ± 0.11
Large fingerlings	B	Dec., '50	104	9.22 ± 0.12	9.31 ± 0.38
	C	Feb., '51	82	9.89 ± 0.12	12.11 ± 0.52

TABLE II. Variation in oxygen level during lethal experiments.

Expt. no.	s_x oxygen level	Expt. no.	s_x oxygen level
	mg. $O_2/l.$		*mg.* $O_2/l.$
E–3	.01	B–6	.05
5	.05	27	.04
12	.05	28	.03
22	.01	44	.05
A–5	.07	41	.04
23	.04	F–4	.03
30	.06	19	.05
C–14	.05	2	.02
17	.04	3	.02
23	.06	5	.01
30	.03	G–5	.02
B–1	.02	7	.03
4	.04	Mean	.035

TABLE III. Resistance times of young speckled trout in three series of experiments, illustrating the basic mortality pattern. (Data derived by combining experiments conducted at similar oxygen levels.)

Fingerlings tested at 0.39 mg. O_2/l. (Expts. B–18, 19, 34)		Fry tested at 1.25 mg. O_2/l. (Expts. E–18, 19, 20)		Fry tested at 1.55 mg. O_2/l. (Expts. E–23, 24)	
Order of death	Time	Order of death	Time	Order of death	Time
	min.		*min.*		*min.*
1	13	1	37	1	250
2	16	2	52	2	510
3	16	3	67	3	770
4	16	4	72	4	1,195
5	17	5	87	5	1,315
6	17	6	87	6	1,485
7	20	7	89	7	1,825
8	21	8	97	8	3,220
9	21	9	101	9	
10	21	10	107	10	
11	22	11	112	11	
12	22	12	117	12	
13	22	13	122	13	Lived
14	23	14	132	14	5,000
15	23	15	132	15	*min.*
16	24	16	147	16	
17	24	17	152	17	
18	25	18	162	18	
19	25	19	162	19	
20	28	20	162		
21	28	21	177		
		22	197		
		23	197		
		24	203		
		25	247		
		26	297		
		27	297		
		28	297		
		29	342		
		30	342		
		31	342		
		32	412		
		33	467		
		34	467		

TABLE IV. Comparison of adjusted arithmetic, geometric and harmonic mean times to death with the observed median times to death. Average figures derived from data on 25 experiments selected at random.

Measure	Average value of statistic ($\bar{x}$), as percentage of the median	s_x	$s_{\bar{x}}$
Arithmetic mean	111	18.7	4.18
Geometric mean	101	13.9	2.84
Harmonic mean	92	15.1	3.08

TABLE V. Comparison of replicate experiments on the resistance of young speckled trout to lethal oxygen experiments. (Data derived from experiments concerned with resistance of fish acclimated to different oxygen levels. Only cases where 100% mortality occurred are considered.)

Stage	Expt. no.	Oxygen level	Resistance times			Signif. diff.
			Rep. 1	Rep. 2	Rep. 3	
		mg. O_2/l.	*min.*	*min.*	*min.*	
Fry	E–16, 17	1.16	75	100	..	nil
	E–18, 19, 20	1.28	145	180	140	nil
Small fingerlings	A–1, 2, 3	0.80	27	36	34	P = .05
	A–8, 9	1.26	235	230	..	nil
	A–15, 16	0.83	48	41	..	nil
	A–23, 24	0.96	145	130	..	nil
	A–25, 26	1.12	430	350	..	nil
	G–12, 13	1.06	102	108	..	nil
Large fingerlings	C–21, 22	0.50	28	32	..	nil
	C–39, 40	0.99	340	420	..	nil

TABLE VI. Resistance times in minutes in nine samples of fry exposed to different lethal oxygen concentrations. Asterisks indicate fish lived over 5,000 minutes. (Fish acclimated to 10.50 mg. O_2/l. $s_x = 0.35$.)

Number	Oxygen levels									
	0.77	0.94	1.10	1.16	1.36	1.43	1.55	1.69	1.77	1.86
1	17	20	25	30	48	50	165	195	240	400
2	18	22	29	30	32	50	165	225	675	**
3	20	24	33	35	60	135	195	270	995	**
4	20	26	33	35	85	175	270	270	2,080	**
5	20	26	37	40	140	195	270	440	**	**
6	21	29	37	45	160	215	440	675	**	**
7	21	29	37	50	170	355	440	995	**	**
8	22	31	41	58	190	405	735	1,150	**	**
9	22	34	48	62	250	465	865	1,150	**	**
10	23	34	55	70	—	600	1,400	**	**	**
11	—	41	—	100	—	—	—	**	—	—
ET_{50}	18	24	31	42	97	180	325	600	—	—

TABLE VII. Changes in median resistance times of fry acclimating from 7.10 mg. O_2/l. to 3.80 mg. O_2/l.

Expt. no.	O_2	Acclimation duration	ET_{50}	S
	mg./l.	*hr.*	*min.*	
D–1	1.02	0	102	1.38
2	1.06	0	108	1.66
3	1.05	8.0	126	1.62
4	1.03	29.0	144	1.53
5	1.07	59.5	189	1.52
6	1.09	71.5	220	1.35
7	1.05	97.5	201	2.07
8	1.06	164.5	200	1.53
9	1.06	177.5	233	1.74
10	1.07	196.5	240	1.32

TABLE VIII. Changes in median resistance times of fry acclimating from 10.50 mg. O_2/l. to 3.93 mg. O_2/l. Fish were exposed to light during acclimation.

Expt. no.	O_2	Acclimation duration	ET_{50}	S
	mg./l.	*hr.*	*min.*	
F–1	0.94	0	21	1.28
2	0.97	0	20	1.24
3	0.97	41.5	69	1.84
4	0.96	70.0	70	2.00
5	0.94	85.5	116	1.27
6	0.96	117.5	119	1.49
7	0.94	132.5	147	1.28
8	0.96	170.5	143	1.50
9	0.94	210.5	202	1.26
10	0.93	259.5	179	1.55
11	0.92	310.0	175	1.35
12	0.94	357.0	217	1.22

TABLE IX. Changes in median resistance times of fry acclimating from 10.50 mg. O_2/l. to 3.93 mg. O_2/l. Fish were kept in dark during acclimation.

Expt. no.	O_2	Acclimation duration	ET_{50}	S
	mg./l.	*hr.*	*min.*	
F–13	0.96	47.0	42	2.08
14	0.96	70.0	52	1.86
15	0.96	88.5	70	2.10
16	0.94	113.0	61	1.69
17	0.96	117.5	66	1.58
18	0.96	136.0	94	2.18
19	0.97	170.5	87	1.91
20	0.95	210.5	163	1.23
21	0.93	259.5	163	2.13

TABLE X. Changes in median resistance times of fry acclimating from 2.46 mg. O_2/l. to 10.00 mg. O_2/l.

Expt. no.	O_2	Acclimation duration	ET_{50}	S
	mg./l.	*hr.*	*min.*	
F–22	1.05	0	360	2.44
23	1.07	17.5	310	1.74
24	1.07	62.0	130	2.87
25	1.06	118.0	59	2.00
26	1.08	900.0	31	1.28

TABLE XI. Median resistance times and extent of mortality in fry exposed to various low oxygen levels. Fish acclimated to 10.50 mg. O_2/l. ($s_x = 0.35$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
E–1	0.77	18	1.12	10	10
2	0.94	24	1.28	11	11
3	1.10	31	1.28	10	10
4	1.16	42	1.38	11	11
5	1.36	97	1.79	9	9
6	1.43	180	1.71	10	10
7	1.54	325	2.25	10	10
8	1.69	600	3.84	11	9
9	1.77	..	..	10	4
10	1.86	..	..	10	2

TABLE XII. Median resistance times and extent of mortality in fry exposed to various low oxygen levels. Fish acclimated to 7.11 mg. O_2/l. ($s_x = 0.20$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
E–12	0.62	22	1.35	10	10
13	0.69	21	1.26	9	9
14	0.92	35	1.28	9	9
15	1.13	82	1.43	10	*
16	1.16	75	1.47	10	10
17	1.16	100	1.20	9	9
18	1.26	145	1.99	12	12
19	1.26	140	1.42	12	12
20	1.28	180	2.76	11	11
21	1.33	190	1.64	10	10
22	1.43	460	2.29	9	9
23	1.55	1,850	4.66	10	6
24	1.56	..	..	9	2
25	1.89	..	..	10	0

TABLE XIII. Median resistance times and extent of mortality in small fingerlings exposed to various low oxygen levels. Fish acclimated to 9.30 mg. O_2/l. ($s_x = 0.33$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
A–1	0.79	27	1.23	10	10
2	0.79	36	1.16	10	10
3	0.82	34	1.16	10	10
4	0.84	23	1.20	10	10
5	0.97	44	1.15	10	10
6	1.04	95	1.78	10	10
7	1.16	135	1.43	10	10
8	1.26	235	1.28	10	10
9	1.27	330	3.19	10	10
10	1.44	500	2.00	10	10
11	1.57	1,150	1.88	10	7
12	1.73	..	..	10	4
13	1.89	..	..	10	0
14	2.09	..	..	10	0

TABLE XIV. Median resistance times and extent of mortality in small fingerlings exposed to various low oxygen levels. Fish acclimated to 6.22 mg. O_2/l. ($s_x = 0.36$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
A–15	0.80	41	1.56	10	10
16	0.84	48	1.30	10	10
17	1.00	107	1.53	9	9
18	1.26	517	2.22	10	8
19	1.33	1,580	2.25	10	7
20	1.36	..	..	10	4
21	1.60	..	..	10	2

TABLE XV. Median resistance times and extent of mortality in small fingerlings exposed to various low oxygen levels. Fish acclimated to 4.56 mg. O_2/l. ($s_x = 0.21$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
A–22	0.86	79	1.49	10	10
23	0.94	145	1.65	11	11
24	0.96	130	1.97	9	9
25	1.10	430	3.05	10	9
26	1.12	350	1.68	10	10
27	1.16	642	..	10	7
28	1.16	335	2.55	10	9
29	1.39	..	..	10	1

TABLE XVI. Median resistance times and extent of mortality in small fingerlings exposed to various low oxygen levels. Fish acclimated to 3.46 mg. O_2/l. ($s_x = 0.17$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
A–30	0.83	54	1.30	10	10
31	0.92	99	1.61	10	10
32	1.00	175	1.83	10	10
33	1.07	330	2.41	10	9
34	1.09	1,260	3.17	10	6
35	1.29	..	..	10	3

TABLE XVII. Median resistance times and extent of mortality in small fingerlings exposed to various low oxygen levels. Fish acclimated to 7.14 mg. O_2/l. ($s_x = 0.27$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
G–1	0.48	21	1.29	7	7
2	0.94	75	1.97	7	7
3	1.05	102	1.68	7	7
4	1.07	108	1.36	7	7
5	1.25	510	2.04	7	7
6	1.39	1,100	3.00	7	5
7	1.57	..	..	7	2
8	1.63	..	..	7	1

TABLE XVIII. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 10.70 mg. O_2/l. ($s_x = 0.22$).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
C–1	0.42	24	1.32	10	10
2	0.58	31	1.20	10	10
3	0.93	91	2.33	11	11
4	1.09	165	1.75	9	9
5	1.17	220	1.93	10	9
6	1.26	199	1.33	10	9
7	1.53	598	2.52	10	10
8	1.78	900	2.71	10	6
9	1.86	1,550	2.29	10	7
10	1.86	..	..	10	3

TABLE XIX. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 9.15 mg. O_2/l. (s_x = 0.41).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
C–11	0.44	27	1.09	10	10
12	0.60	28	1.03	10	10
13	0.71	75	1.37	10	10
14	0.96	186	1.69	10	10
15	1.04	305	1.74	9	9
16	1.19	305	1.76	10	9
17	1.27	390	1.74	10	10
18	1.46	1,210	1.71	11	10
19	1.63	..	..	9	4
20	1.76	..	..	10	0

TABLE XX. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 5.16 mg. O_2/l. (s_x = 0.47).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
C–21	0.47	28	1.13	10	10
22	0.53	32	1.17	10	10
23	0.76	148	1.26	10	10
24	0.96	305	1.45	10	*
25	1.13	600	2.18	10	10
26	1.17	800	2.53	10	8
27	1.26	1,250	2.61	10	*
28	1.44	..	..	10	4

TABLE XXI. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 3.59 mg. O_2/l. (s_x = 0.51).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
C–29	0.41	30	1.21	10	10
30	0.57	35	1.11	10	10
31	0.74	137	1.42	9	7
32	0.96	339	1.48	10	6
33	1.04	485	1.72	10	8
34	1.10	1,200	3.86	10	6
35	1.15	..	..	10	4

TABLE XXII. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 2.52 mg. O_2/l. (s_x = 0.42).

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
C–36	0.42	30	1.21	10	10
37	0.60	34	1.23	10	10
38	0.73	179	1.39	10	*
39	0.97	340	1.60	10	6
40	1.00	420	1.96	11	11
41	1.07	1,310	3.35	10	6
42	1.09	..	..	10	1

TABLE XXIII. Intercepts and slopes of regression lines relating median resistance times to oxygen levels for samples of young speckled trout acclimated to different environmental oxygen levels.

Stage	Experimental series	Acclimation level	a	b	Sb
		mg. O_2/*l.*			
Fry	E	10.50	−0.977	2.23	0.088
		7.11	−0.444	2.09	0.178
Small fingerlings	A	9.30	−0.504	2.28	0.130
		6.22	−0.881	2.96	0.380
		4.56	−0.090	2.74	0.364
		3.46	−0.921	3.19	0.161
	G	7.14	−0.787	2.74	0.191
Large fingerlings	C	10.70	+0.692	1.36	0.059
		9.15	+0.560	1.70	0.149
		5.16	+0.511	2.01	0.094
		3.59	+0.143	2.49	0.377
		2.52	+0.357	2.28	0.537

TABLE XXIV. Incipient lethal levels of young speckled trout acclimated to different oxygen levels.

Stage	Experimental series	Acclimation level	Incipient level level			Mortality limits	
			ED_{50}	S	K[a]	5%	95%
		mg. O_2/*l.*	*mg.* O_2/*l.*	*mg.* O_2/*l.*		*mg.* O_2/*l.*	*mg.* O_2/*l.*
Fry	E	10.50	1.75	1.07	5	1.93	1.57
		7.11	1.55[b]	..	2	..	..
Small fingerlings	A	9.30	1.63	1.08	4	1.87	1.43
		6.22	1.39	1.14	4	1.72	1.13
		4.56	1.25	1.07	5	1.39	1.11
		3.46	1.19	1.09	5	1.37	1.02
	G	7.14	1.53	1.11	4	1.78	1.26
Large fingerlings	C	10.70	1.86[b]	..	2	..	..
		9.15	1.59	1.07	3	1.76	1.43
		5.16	1.38	1.13	3	1.67	1.12
		3.59	1.13[b]	..	1	..	..
		2.52	1.06	1.04	3	1.10	1.01
Large fingerlings (tested in light)		7.09	1.33	1.04	9		
Large fingerlings (tested in dark)		7.09	1.32	1.07	5		

[a]Number of experiments where more than 0% and less than 100% mortality occurred (cases where 100% effects could be used, according to Litchfield and Wilcoxen's (1949) method, included).

[b]Incipient lethal levels estimated by inspection.

TABLE XXV. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 7.09 mg. O_2/l. ($s_x = 0.27$). Tests were conducted with fish in darkness 24 hours before and during experiments.

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
B–1	0.44	22	1.50	7	7
2	0.44	18	1.23	7	7
3	0.54	28	1.31	7	7
4	0.56	31	1.20	7	7
5	0.60	39	1.23	7	7
6	0.61	37	1.36	7	7
7	0.71	56	1.65	7	7
8	0.71	83	1.94	7	7
9	0.80	157	1.54	7	7
10	0.99	570	2.22	7	*
11	0.99	505	3.76	7	*
12	1.08	655	1.21	7	*
13	1.26	1,630	1.59	7	5
14	1.28	3,130	2.46	7	4
15	1.29	..	..	7	3
16	1.33	4,900	1.19	7	4
17	1.36	5,000	1.20	7	4

TABLE XXVI. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 7.09 mg. O_2/l. ($s_x = 0.27$). Tests were conducted with fish exposed to light 24 hours before and during experiments.

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
B–18	0.37	21	1.13	7	7
19	0.39	22	1.23	7	7
20	0.69	34	1.31	7	7
21	0.69	46	1.74	7	7
22	0.93	139	1.31	7	7
23	0.93	128	1.93	7	*
24	1.02	340	1.30	7	7
25	1.02	420	2.39	7	7
26	1.07	740	3.00	7	7
27	1.07	305	1.84	7	7
28	1.22	510	..	7	7
29	1.29	1,650	2.14	7	6
30	1.30	775	1.28	7	7
31	1.30	900	..	7	6
32	1.33	..	..	7	3
33	1.36	11,900	1.33	7	4

TABLE XXVII. Median resistance times and extent of mortality in large fingerlings exposed to various low oxygen levels. Fish acclimated to 7.09 mg. O_2/l. (s_x = 0.27). Tests were conducted with fish exposed to light 30 minutes before and during experiments.

Expt. no.	O_2	ET_{50}	S	N	M
	mg./l.	*min.*			
B–34	0.40	18	1.28	7	7
35	0.49	24	1.33	7	7
36	0.62	44	1.39	7	7
37	0.62	27	1.07	7	7
38	0.69	48	1.40	7	7
39	0.73	58	1.65	7	7
40	0.84	163	1.31	7	7
41	0.90	120	1.39	7	7
42	0.93	114	1.29	7	7
43	1.03	390	1.71	7	7
44	1.04	225	1.67	7	7
45	1.06	370	1.17	6	6
46	1.08	378	1.16	6	6
47	1.09	310	1.23	7	*
48	1.25	1,400	2.50	7	6
49	1.37	3,500	1.69	7	5
50	1.37	..	..	7	3

TABLE XXVIII. Comparison of slope functions (S values) experiment on large fingerlings conducted in the light and in darkness. (Data from Tables XXV–XXVII.)

	S		
Lethal level	Expts. in dark	Expts. in light 24 hr.	Expts. in light 30 min.
mg.O_2/*l.*			
0.42	1.50	1.23	1.28
0.71	1.65	1.31	1.40
1.01	2.22	2.39	1.71
1.07	1.21	1.84	1.16
1.25	1.59	2.14	2.50
$\bar{X}$	1.63	1.82	1.61

TABLE XXIX. Maximum rates of oxygen uptake, determined at different oxygen levels, in young speckled trout acclimated to different oxygen levels.

Stage	Weight	Oxygen level	Acclim. level	Oxygen uptake	Acclim. level	Oxygen uptake
	g.	*mg.* O_2/*l.*	*mg.* O_2/*l.*	*mg.* O_2/*l.*	*mg.* O_2/*l.*	*mg.* O_2/*l.*
Fry	2.2	2.00		76.5		93.5
		2.54		110.5		157.0
		3.88	10.0	209.0	3.0	259.5
		6.88		285.0		301.0
		8.50		323.5		331.0
Fingerlings	15.6	1.80		62.0		76.5
		2.82		107.5		127.5
		4.55	10.0	177.0	3.0	189.5
		5.58		233.0		213.0
		6.72		253.5		249.5
Yearlings	26.5	2.14		50		75
		2.86	7.0	100	3.5	100
		4.29		135		155
		7.15		210		205
	23.3	2.14		55		55
		2.86	7.0	80	3.5	115
		4.29		145		170
		7.15		250		225

A Method for Removing the Effect of Recruitment on Petersen-type Population Estimates[1, 2]

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ABSTRACT

A regression analysis, which is based on time changes in the ratio of the number of marked fish in the daily catch to the total daily catch, was used to estimate initial population size. This method eliminates overestimation caused by recruitment.

PROCEDURE

Many Petersen-type estimates of fish populations based on seasonal recovery of marked individuals are found to be too high. This is due in part to recruitment to the catchable population during the period being considered. Methods which have been used in the past to eliminate or correct for recruitment have been reviewed by Ricker (1948).

Under suitable assumptions, namely (1) equal rates of catchability and natural mortality at any one time for both marked and unmarked individuals, (2) random dispersal of marked fish, and (3) constant absolute rate of recruitment to the catchable portion of the population, it is possible to estimate the initial population by plotting the ratio of the number of marked fish in the daily catch to the total daily catch against the number of days after marking has ceased. Effects of this ratio's non-normality may be partially removed by applying a transformation such as the arcsin (Bartlett, 1936) or the more common logarithmic. The former has been used here. The slope of the best fitting linear regression line will be negative, corresponding to a decrease in the computed ratio as time passes. Number of fish marked divided by the Y-intercept gives the initial population estimate.

EXAMPLE

This method has been applied to marking data collected in 1953 from a population of bluegills, common sunfish, and hybrids between the two in Flora Lake, Vilas County, Wisconsin. Although this type of grouping has been shown to be inadvisable (Ricker, 1948), identification difficulties preclude separate treatments.

The fish were caught in fyke nets and were marked by removal of left pelvic fins, between the dates July 2 and July 6. Subsequent catches were made in the same nets, and all fish netted were killed. These samples were taken between July 9 and October 18. The data are presented in Table I.

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[2]Data used were taken from a study supported in part by a grant from the Wisconsin Alumni Research Foundation.

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TABLE I. Data used in making a marked-fish regression analysis of a population of bluegills, common sunfish, and hybrids between the two.

Date	Days after end of marking	Fish in sample	Marked fish in sample / Total fish in sample	Arcsin of $\sqrt{\text{ratio}}$	Marked fish removed by netting	Estimated nat. mort. of marked fish	No. of marked fish remaining at day's end
July 6	...	...	...	...	...	9[a]	3,220
9	3	86	0.1279	20.96	11	15	3,194
10	4	733	0.0559	13.69	41	5	3,148
11	5	618	0.0825	16.64	51	5	3,092
12	6	703	0.0768	16.11	54	5	3,033
13	7	673	0.1382	21.81	93	5	2,935
14	8	948	0.1298	21.13	123	4	2,808
15	9	244	0.0984	18.24	24	4	2,780
18	12	225	0.1156	19.91	26	13	2,741
19	13	622	0.1495	22.79	93	4	2,644
20	14	540	0.1444	22.30	78	4	2,562
21	15	650	0.1538	23.11	100	4	2,458
22	16	907	0.1246	20.70	113	4	2,341
23	17	252	0.0675	15.12	17	4	2,320
24	18	1019	0.1109	19.46	113	4	2,203
25	19	549	0.0874	17.16	48	3	2,152
26	20	567	0.1376	21.81	78	3	2,071
27	21	438	0.1027	18.72	45	3	2,023
28	22	183	0.0601	14.18	11	3	2,009
29	23	537	0.1117	19.55	60	3	1,946
30	24	98	0.0714	15.45	7	3	1,936
31	25	795	0.0969	18.15	77	3	1,856
Aug 2	27	387	0.0388	11.39	15	6	1,835
3	28	233	0.1030	18.72	24	3	1,808
5	30	250	0.0800	16.43	20	6	1,782
6	31	443	0.1061	19.00	47	3	1,732
8	33	580	0.1052	18.91	61	5	1,666
13	38	628	0.0685	15.12	43	13	1,610
14	39	151	0.0464	12.39	7	2	1,601
15	40	305	0.1836	25.40	56	2	1,543
16	41	36	0.1944	26.13	7	2	1,534
20	45	91	0.1209	20.36	11	9	1,514
21	46	1025	0.0498	12.92	51	2	1,461
22	47	308	0.0454	12.25	14	2	1,445
24	49	308	0.0454	12.25	14	4	1,427
27	52	51	0.0980	18.24	5	7	1,415
30	55	78	0.0641	14.65	5	6	1,404
31	56	193	0.0518	13.18	10	2	1,392
Sept 2	58	290	0.1345	21.47	39	4	1,349
27	83	54	0.0741	15.79	4	51	1,294
Oct 18	104	132	0.0379	11.24	5	41	1,248
Totals		16,930			1,701	280	

[a]During marking.

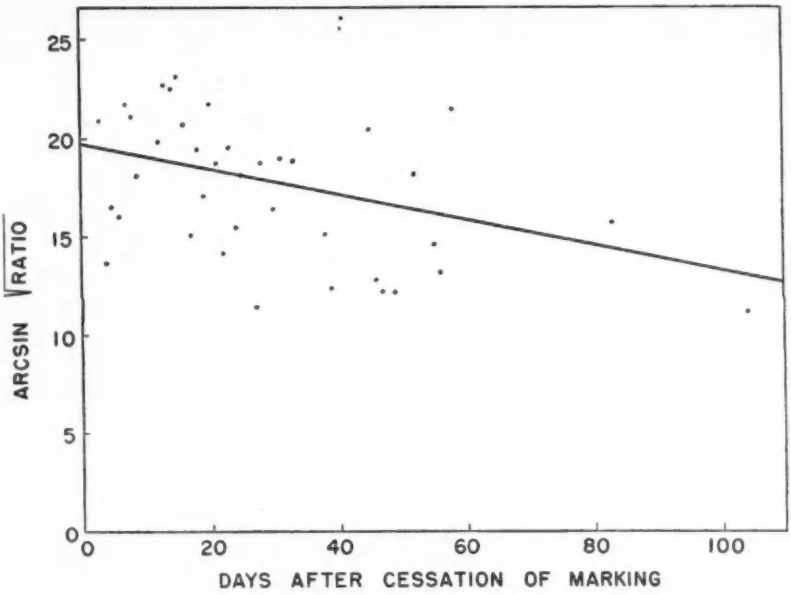

FIGURE 1. Regression of the transformed ratio on days after cessation of marking.

Points were plotted as discussed earlier, and a linear regression was fitted (Fig. 1). The equation for this line is given by:

$$Y = 19.7614^\circ - 0.0645269\ X$$

The Y-intercept was converted to the equivalent ratio 0.11435. Now, if mortality during the marking period is neglected, 3,229 fish marked divided by 0.11435 gives an estimate of 28,238. Similarly, if marking period mortality is approximated (Table I), the estimate becomes 28,159.

Since all fish taken after July 6 were removed, sums of the daily totals are used in computing a conventional Petersen estimate as follows:

$$N = \frac{(\text{Marked fish released})\ (\text{Seasonal catch})}{\text{Marked fish recaptured}}$$

$$= \frac{(3{,}229)\ (16{,}930)}{1{,}701} = 32{,}138$$

Appropriate confidence limits are given in Table II.

An average annual mortality rate of 0.427 was calculated from age frequencies. Lacking information on the seasonal distribution of mortality, a daily rate of 0.00153 can be assumed and an estimate of recruitment to catchable size can be made for the sampling period. This was done as indicated in Table III.

TABLE II. Comparison of conventional and modified Petersen estimates.

	Conventional	Modified	
Population estimate	32,138	28,238[a]	28,159[b]
95% confidence interval			
Lower limit	30,725	23,459	23,394
Upper limit	33,623	34,778	34,681

[a]Natural mortality during marking period ignored.
[b]Natural mortality during marking period estimated.

TABLE III. Estimation of recruitment to the catchable portion of the population for the period July 6, 1953 to October 18, 1953.

(1)	Estimated population as of July 6	28,159
(2)	Estimated population as of October 18	24,468[a]
(3)	Removal	16,930
(4)	Estimated natural mortality	3,457
(5)	(3)+(4)	20,387
(6)	(1)−(5)	7,772
(7)	(2)−(6) = recruitment	16,696

[a]N = 1248 (Table I) divided by 0.051005 (computed ratio after 104 days).

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The Skeena River Salmon Fishery, with Special Reference to Sockeye Salmon[1]

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ABSTRACT

The general history of the Skeena River commercial salmon fishery is presented from 1877 to 1948. The changes in fishing areas, seasons and fishing methods are described, together with the trends in the catches obtained. The most accurate data pertain to the important sockeye salmon gill-net fishery. The sockeye catch attained a maximum of 187,000 cases in 1910 and since then has declined to a minimum of 28,000 cases in 1933 and 1943. In recent years the catches have tended to level off. The pink salmon catches declined markedly after 1930. The chum catches also appear to have declined in recent years. Whether or not the spring and coho salmon catches have declined is not known. The size of the sockeye catch appears to be the best available measure of the relative size of the population. An analysis of the age cycles in the catch of sockeye and pink salmon did not reveal a practical basis for prediction. Some possible changes in the fishing regulations are discussed and the need for more data on the fluctuations in the size of the stocks during the fresh water phase is stressed.

INTRODUCTION

THE SALMON of the genus *Oncorhynchus* have long been an important source of food around the shores of the North Pacific Ocean. Before white settlement, they were used for food and barter by the Indians. Recent advances in fishing and handling methods have made them the natural resource for an important and highly developed industry.

The sockeye salmon (*O. nerka*) is the most valuable of the five species of Pacific salmon. It is concentrated in the large rivers that have suitable nursery lakes at their headwaters. In British Columbia the Skeena River is of intermediate rank, with a production of raw fish for canning worth about $2,000,000 annually. In addition, the whole benefit includes the value of the salmon handled fresh and frozen. This is hard to determine. Some of the fish are caught so far from the river in which they spawn that it is difficult to credit them to their proper destination.

The sockeye salmon constitutes about 30 per cent of the number and 50 per cent of the value of the salmon canned from the Skeena River fishery. Pink salmon (*O. gorbuscha*) is also important, but in recent years the catch has been greatly reduced. Spring (*O. tshawytscha*) and coho (*O. kisutch*) are prominent in the fresh and frozen trade. The chum salmon (*O. keta*) catch is small and of little importance in the Skeena River.

The records of the commercial fishery on the Skeena River provide the only available data on the fluctuations in these salmon populations. Since the fish are exploited assiduously near the river mouth during almost the whole of the relatively short migration period, the size of the catch should in general indicate the size of the population. Therefore from a study of the fluctuations in the commercial catch and in the intensity of the fishing effort it was hoped that an indication of the change in the stock could be obtained. Since the catches of both sockeye and pink salmon have appeared to fluctuate, the long-term trends and short-term cycles were also analysed to determine what changes may have occurred in these populations and whether our present knowledge is exact enough to provide useful predictions of future catches. The catches of the other three species of salmon, spring, coho and chum, are given but, owing to the varied

nature of these fisheries, the present state of the population which spawn in the Skeena River can not be clearly established.

The work reported here was a part of the Fisheries Research Board's five-year Skeena River Salmon Investigation, conducted in 1944–48. Statistics available through 1948 were used for the analysis of trends in catch and fishing effort, and the computations made from them have not been altered. At time of publication five more years' data have become available. However, to incorporate this period into the analysis would involve complete reworking of most of the computations, so it has seemed best to present the material substantially as it was available in 1948. More recent years will be reported in detail by the investigators now concerned with the Skeena fishery. The present paper makes only a few brief references to recent trends, at places where they seem to support or modify the interpretation of earlier information.

ACKNOWLEDGMENTS

This study was carried out from 1946 to 1948 under the direction of Dr. R. E. Foerster, then Director of the Pacific Biological Station, and Dr. A. L. Pritchard, then in charge of the Skeena River Salmon Investigation. Thanks are due to Messrs. W. Tait, P. Tourner and R. Ferguson for much of the detailed recording and assembling of data.

The officers of the Federal Department of Fisheries and the managers of the canneries on the Skeena River, namely Sunnyside, Cassiar, Carlisle, North Pacific, Inverness and Port Edward, have been most cooperative and helpful in making available past records.

The writer is greatly indebted to several fellow workers at the Pacific Biological Station, in particular to Dr. W. E. Ricker, for the many helpful suggestions in the preparation of this paper.

HISTORY OF THE FISHERY

Development of Canneries and Fresh-Fish Establishments

The first cannery on the Skeena River, Inverness, was built in 1877, in which year 3,000 cases of salmon were canned. The number of canneries increased to a maximum of fifteen operating between 1917 and 1920 and in 1926. Since the latter date the number has decreased. From 1944 to 1948 there were seven.

The first fresh-fish establishment was issued a licence in 1910, but it was not until 1914 that the Canadian Fish and Cold Storage plant was completed and the first frozen fish shipped east by rail. Since then the number of fresh-fish establishments has increased until at the present time there are ten operating, of which three have freezing and cold-storage facilities.

The number of plant licences issued from 1877 to 1948 is given in Table I.

The reduction in the number of canneries operating since 1926 was accompanied by a concentration of equipment in certain canneries with a consequent increase in efficiency and capacity. A comparison between the capacities of the twelve canneries operating in 1910 and the seven canneries operating in 1945

TABLE I. Number of licences issued to canneries and fresh fish establishments, 1877–1948. (Records are not available for all years prior to 1905.)

Year	Canneries[a]	Fresh fish establishments[b]	Year	Canneries[a]	Fresh fish establishments[b]
1877	1	..	1921	13	3
1878	2	..	1922	13	3
			1923	13	3
1883	5	..	1924	13	3
			1925	13	3
1885	2	..	1926	15	7
			1927	13	7
1890	7	..	1928	11	7
			1929	11	7
1895	7	..	1930	11	7
			1931	8	7
1900	10	..	1932	10	7
			1933	10	7
1905	.12	..	1934	9	7
1906	14	..	1935	9	7
1907	13	..	1936	8	7
1908	13	..	1937	7	7
1909	12	..	1938	6	7
1910	12	1	1939	6	7
1911	12	1	1940	7	8
1912	12	1	1941	7	9
1913	13	1	1942	6	9
1914	13	2	1943	8	9
1915	13	2	1944	7	9
1916	14	2	1945	7	9
1917	15	2	1946	7	10
1918	15	2	1947	7	10
1919	15	2	1948	7	10
1920	15	3			

[a]From Annual Reports of Federal Department of Fisheries.
[b]From files of Federal Department of Fisheries, Prince Rupert.

indicated that in the latter period more than twice as many fish were handled and that each cannery processed more than three times as many fish as in the earlier period. In the face of the decline in parts of the Skeena River salmon catches, the increased amount which is now canned is only possible by an increase in the number of fish brought in from other areas.

TREND IN FISHING EFFORT

REGULATIONS REGARDING AREA

The *Skeena gill-net area*, described in the Special Fishery Regulations of B.C. (1949), is shown in Figure 1 bounded by double lines. Formerly the area extended farther upriver and not as far seaward. Thus, in 1910 the river boundaries were about 20 miles up the Skeena and 8 miles up the Ecstall River, in 1925 about 12 miles up the Skeena and 8 miles up the Ecstall and in 1935 about 9 miles up the Skeena and 3 miles up the Ecstall. The 1935 limits are the present

river boundaries for spring and coho fishing, but during the sockeye season the boundary is lowered by about 5 miles to extend between Mowitch and Veitch points. This prohibits fishing for sockeye in the Ecstall River. With the reduction of the river area in 1935 the ocean area was extended from a line running west of Ryan Point to one west of Finlayson Island. Thus the present Skeena gill-net

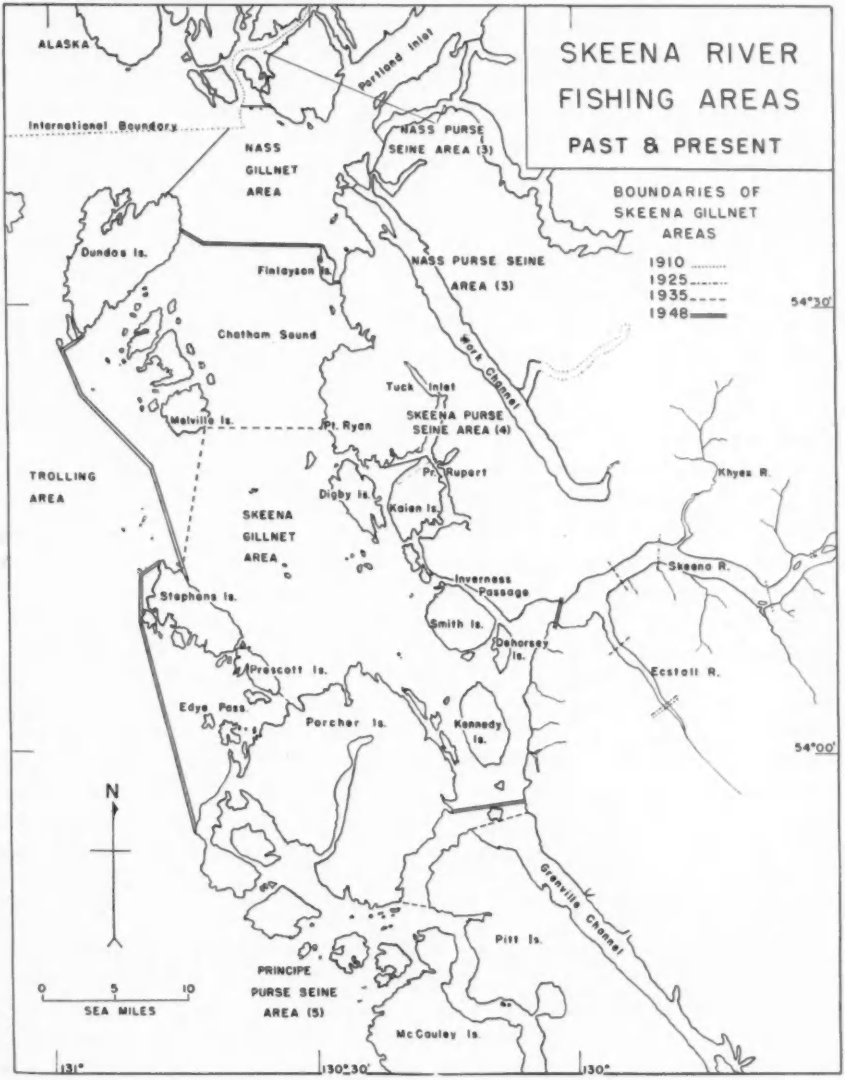

FIGURE 1. Map of Skeena River commercial salmon fishing areas—past and present.

area extends from the river boundaries to Porcher Island on the south, Finlayson and Dundas Islands on the north, and Stephens Island on the west. The above changes in fishing boundaries are also shown in Figure 1.

Within the Skeena gill-net area the majority of the sockeye fishing occurs in the river mouth, in Inverness Passage, west of Smith Island, in Edye Passage and off Finlayson Island. These fishing sites are of biological interest when related to the path of the freshwater runoff from the Skeena River (Cameron, 1948).

The neighbouring salmon fishing areas are also shown in Figure 1. The Nass gill-net area lies to the north. The closest purse-seine area to the Skeena River is Tuck Inlet, No. 4, which has not been fished in recent years. To the north, purse-seine area No. 3 is divided into five parts off the mouth of the Nass River. Area No. 5 lies to the south of the Skeena gill-net area. Trolling is permitted throughout the whole region but the major part is carried on outside Dundas, Stephens and Porcher Islands.

REGULATIONS REGARDING SEASON

Prior to 1935 the sockeye fishing season commenced on June 20. Since then the season has commenced on the last Sunday in June, which means that a variation of up to six days might exist in the actual starting date from year to year. The opening has been delayed in two instances owing to strikes. In 1932 fishing did not start until July 11 (Indian fishermen started July 3), a loss of fifteen days fishing, and in 1945 it did not start until July 1, a loss of seven days. The closing date is set each year by the Federal Department of Fisheries and has varied from August 13 to August 22. The opening and closing dates for sockeye salmon from 1931 to 1948 are listed in Table II.

TABLE II. Skeena sockeye fishing seasons, 1931–48.

Year	Opening date	Closing date	Year	Opening date	Closing date
1931	June 20	Aug. 21	1940	June 30	Aug. 16
1932	July 11	20	1941	29	22
1933	June 20	18	1942	28	21
1934	20	17	1943	27	20
1935	July 1	16	1944	25	18
1936	June 28	20	1945	July 1	17
1937	July 1	13	1946	June 30	16
1938	June 26	19	1947	29	15
1939	25	18	1948	27	20

No predetermined dates are set for the spring salmon gill-net fishery, which starts when the first spring net is used, usually in April, and ends when the migration is over in the latter part of July. The river boundary is moved downstream as soon as the sockeye season opens. The coho gill-net season opens 48 hours after the closing of the sockeye season and closes when the migration is over in the latter part of September. The river boundary is moved upriver for

the coho fishing one week after the closing of the sockeye season. The weekend closed period for gill-net fishing is from Friday at 6 p.m. to Sunday at 6 p.m.

REGULATIONS REGARDING GEAR

The regulations for gear require that a gill-net shall not exceed 200 fathoms in length and 50 meshes of uniform size in depth. There is no minimum limit for the mesh size of sockeye gill-nets. The mesh of other salmon gill-nets is not less than 6½ inches extension measure when in use. The nets must not be used so as to enclose any bay, cove, creek or inlet, and in all cases one-third of the width of any such channel shall remain open and unobstructed for the passage of fish. In commercial fishing no salmon weighing less than 3 pounds in the round (or 2½ pounds dressed) can be retained.

When the current regulations are compared with those laid down in 1894 only a few minor changes appear (Carrothers, 1941). For example, in 1894 the weekly closed period was from 6 a.m. Saturday to 6 p.m. Sunday, the spring salmon net mesh size was not less than 7¾ inches and the sockeye 5¾ inches, and the sockeye season was open from July 1 to August 25.

Operating Methods of the Gill-net Fishery

Salmon are caught by three types of gear, gill-net, purse-seine and troll. However for the Skeena salmon populations, particularly the sockeye salmon, the gill-net is the most important method and will now be treated in detail.

DESCRIPTION OF A GILL-NET

A gill-net is a long rectangular net of fine twine with a cork line along the upper edge and a lead line along the lower. The mesh sizes in use at present are 8½ to 9 inches for spring salmon, 6½ to 7 inches for coho salmon and 5½ to 5¾ inches for sockeye salmon. When set, the net forms a vertical barrier about 1,200 feet in length (200 fathoms) and 25 feet in depth in the path of the incoming fish, with only the cork line showing on the surface of the water. The size of mesh is large enough to allow a fish to thrust its head through but is small enough to prevent the body passing. When a fish hits the net, it either attempts to back up and so is caught by the gills, or it drives through and is firmly caught around the body ahead of the dorsal fin. The net is usually set at right angles to the direction of flow of the tide or current, and is allowed to drift with it. It is thus called a "drift-net".

CHANGES IN EFFICIENCY OF GEAR AND OF FISHERMEN

At the beginning of the century all gill-net boats on the Skeena River were equipped with sails and were towed to the fishing grounds by power-driven tugs. There were usually two men on each boat. Prior to 1924 it was unlawful to use boats other than those propelled by sails or oars for salmon gill-net fishing in the northern area of British Columbia. From 1924 to 1935 gasoline engines were installed in many of the old sail boats and new power-driven boats were built. Since 1942 no sail boats have operated on the Skeena River. The gill-net boats are about 30 feet long and powered by engines ranging from 10 to 110 h.p. In 1942 the power-driven "net-drum" came into general use for lifting

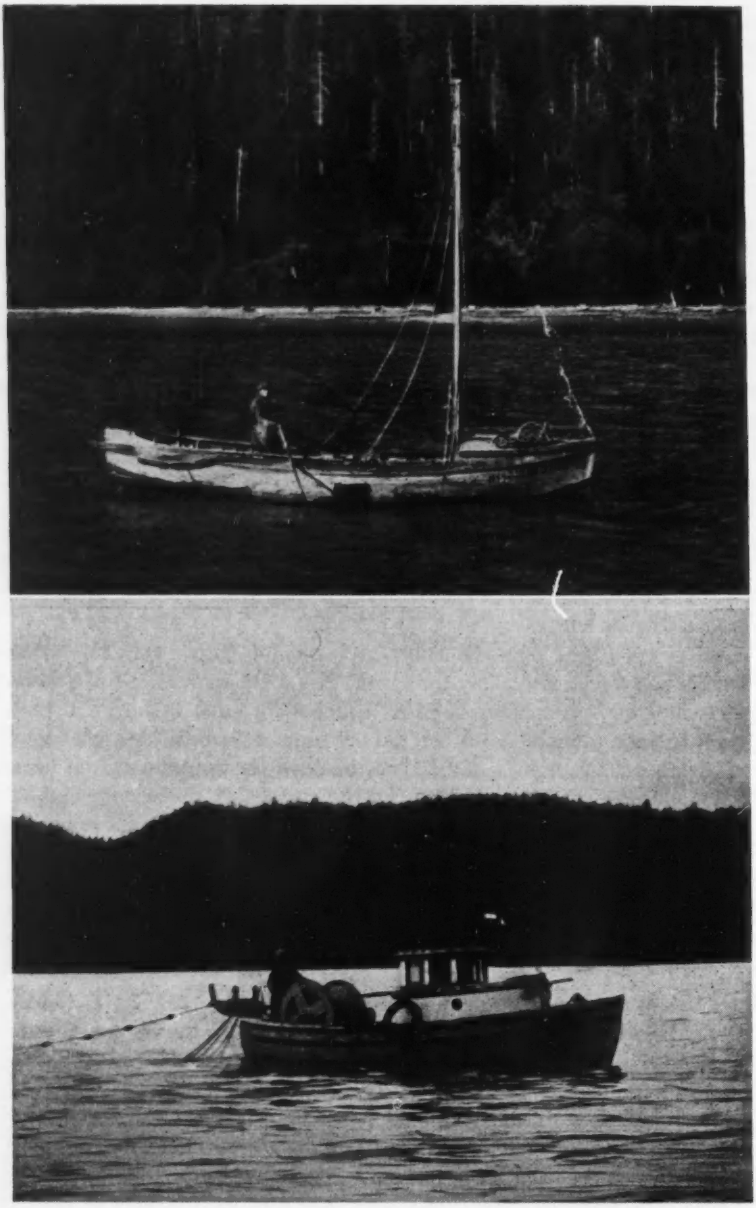

FIGURE 2. The old and new types of gill-net fishing boats. *Above*: sail boat; *below*: gasoline boat with drum.

the nets. The old and the new types of salmon gill-net boats are illustrated in Figure 2.

The number of gill-net boat licences issued each year for the Skeena area is given in Table III and presented in Figure 3. From the number of licences issued it appears that the effort increased up to 1919 and since 1933 has fallen off. The decline is probably associated with a reduction in the availability of fish and an increase in the efficiency of the gear.

The introduction of the gas boat in 1924 brought a change in fishing methods, in that the boats were able to move around faster and make more sets by doubling back and resetting in the most favourable locations. A comparison of the records available at one cannery shows a small increase in the catch of the gas boat over the sail boat. For example during the years 1930 to 1933 inclusive, 96 gas boats averaged 1,260 sockeye per boat per year while 41 sail boats averaged 1,163. The automatic "net-drum" speeded up the netting operations, with the result that as

TABLE III. Skeena gill-net boat licences issued from 1877 to 1948. (Figures are not available for all years prior to 1911.)

Year	Total[a]	Year	Total[a]	Japanese[b]	Gas boats[b]	Adjusted total[c]
1877	40	1922	1,091	642	...	1,321
1878	80	1923	900	578	...	1,101
...	...	1924	941	385	18	1,048
1883	160	1925	1,067	327	65	1,134
...	...	1926	1,129	295	75	1,184
1890	269	1927	1,195	295	162	1,253
...	...	1928	1,208	295	257	1,299
1900	448	1929	1,143	295	263	1,214
...	...	1930	1,202	295	637	1,301
1905	781	1931	1,076	295	607	1,184
1906	870	1932	1,119	295	760	1,237
1907	700	1933	1,218	295	669	1,318
1908	863	1934	1,164	295	740	1,276
...	...	1935	1,053	295	842	1,184
1911	850	1936	970	295	882	1,109
1912	850	1937	850	295	840	999
1913	850	1938	1,049	295	1,043	1,199
1914	850	1939	844	295	841	994
1915	962	1940	926	295	922	1,076
1916	868	1941	981	295	976	1,131
1917	788	1942	775	...	774	775
1918	889	1943	749	...	749	749
1919	1,153	1944	725	...	725	725
1920	954	1945	787	...	787	787
1921	1,109	1946	877	...	877	877
		1947	750	...	750	750
		1948	833	...	833	833

[a]From Annual Reports of Federal Department of Fisheries.
[b]From files of Federal Department of Fisheries, Prince Rupert.
[c]Total adjusted by rating gas boats 1.0, sail boats 0.9; and Japanese fishermen 1.5, Indian and White fishermen 1.0.

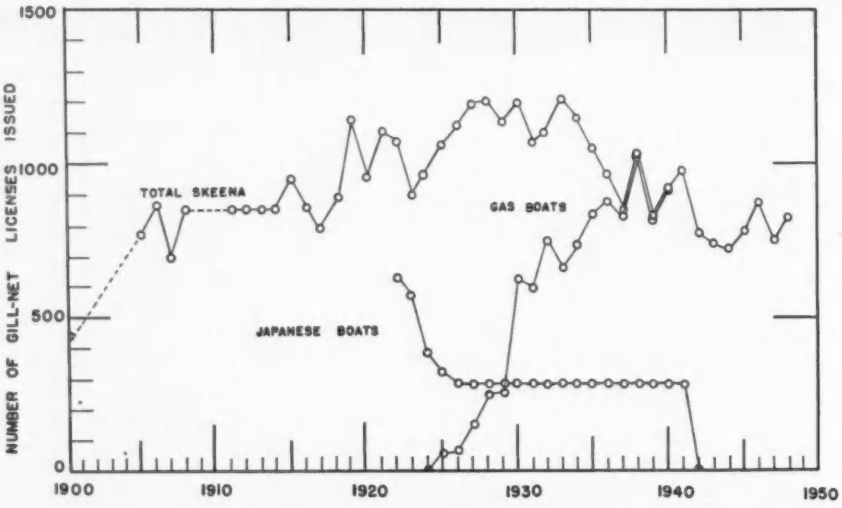

FIGURE 3. The total number of gill-net licences issued in the Skeena River area up to 1948, showing the introduction of the gasoline boats and the decrease in the Japanese boats.

many as four times the number of sets could be made in the same period of time. The result has been that more sets can now be made at each high and low tide with a great reduction in manual labour.

A comparison of the catches of the three groups of fishermen, namely, Japanese, Indian and White, indicates that during the period 1930–36 the Japanese, who comprised about one-third of the fishermen of a cannery fleet, caught about twice as many sockeye per boat per year as either the Whites or the Indians. This difference in efficiency was reduced when the latter two groups of fishermen acquired and learned to operate the new gasoline boats. Thus a similar comparison for the years 1937–41 shows that the Japanese caught only 1.4 times as many fish as the Whites or the Indians.

To accomplish this greater catch the Japanese fished from 2 to 10 days longer and caught from 300 to 900 more fish per season. Since their daily catch was 5 to 8 fish higher, they probably also fished longer each day. From 1922 to 1926 the number of Japanese licences gradually decreased from over 600 to less than 300. The emigration of the Japanese fishermen from coastal areas in 1941 lowered the fishing intensity during 1942 and 1943 while new Indian fishermen were being recruited. This partly accounts for the extremely low catches in these two years.

SELECTIVITY OF THE GILL-NET FISHERY

The gill-net fishery is selective for size of fish, both because of the uniformity of mesh size and because of the time of the fishing in relation to the progress of the run. This results in the commercial sockeye catch or any samples taken from

it being unrepresentative of either the total population or of the spawning escapement as regards size, age and sex.

A study of age and sex distribution of the sockeye salmon catch for the years 1926 to 1940 (Withler, 1945) has shown that the percentage of the 4_2 age-group[2] (particularly the females) increases throughout the fishing season while that of the 5_2's (particularly the males) decreases, with the result that the females comprise an increasing proportion of the catch. This is because the males of each group migrate earlier than the females, and the older age-groups precede the younger ones. In sockeye salmon the males tend to mature at a younger age than the females, with the result that there is a higher proportion of females in the older age-groups (5's and 4's), whereas the 3-year-olds are almost all males. These small precocious males, less than 19 inches in length, are usually called "jacks" and are not normally caught in the gill-nets, but show up on the spawning grounds as "runts".

In the Skeena fishery the commercial sockeye catch has always contained more females than males in the 5_2 age-group (Clemens, 1950). During the period from 1915 to 1935, when the season opened on June 20, the average percentage of females was 56. From 1936 to 1948, when the opening date was the last Sunday in June, the average percentage was 63. Apparently more males than females run prior to the opening of the fishing season. In the case of the 4_2 age-group, which runs later, the males averaged 53 per cent of the catch from 1915 to 1929, at which time the mesh size was reduced so that the smaller females might be caught. Since then, from 1930 to 1948, the average for males has dropped to 43 per cent. The jacks appear to run later in the season than the other groups.

The selective action of the fishery was most striking in 1947, when a large proportion of the spawning population was jacks. Scale samples taken from sockeye caught by the commercial fishery, using gill-nets with a mesh size of 5¾ inches, contained only 6 jacks in 1,365 fish, or 0.3 per cent. Females made up 66 per cent of these samples. The number of jacks caught by the tagging boat, up to July 27, using a purse-seine with a mesh size of 3½ inches, was 360 out of 2,328 or 15 per cent. Since the percentage of jacks was increasing as the season progressed, the tagging boat would probably have taken a greater number of jacks if fishing had continued until August 15. When the fish passed upriver the number of jacks in the escapement was high. At Moricetown Falls, where most of the jacks are in the 4_3 age-group, it was estimated that they comprised about one-quarter of the run and at the Babine River counting fence, where most of the jacks are of the 3_2 age-group, they made up 50 per cent of the total count.

To judge from smaller samples of pink and chum salmon taken from the gill-net fishery from 1946 to 1948, the effect of selection was apparently the reverse of that for sockeye. In pink salmon the selection of males was particularly high, probably because of their shape and large size. The maturing male develops a pronounced hump on the back and a long hooked nose, which are

[2]A fish of the 4_2 age-group is one that went to sea early in its second year and returned to spawn in its fourth year.

absent in the female. The samples in 1946 contained 90 per cent males; in 1947 it was 75 per cent and in 1948, 65 per cent. In the case of chum salmon the percentage of males ranged from 50 to 75. For both spring and coho salmon the sex ratio in these samples was approximately equal, but many jacks are observed in the spawning streams.

EFFECTS OF WEATHER

Fishermen believe that the weather affects sockeye salmon in the following manner: southeasterly winds, bringing rain and storms, drive the fish deeper, where they are either caught near the lead line or miss the net altogether. Westerly winds, bringing good weather, cause the fish to leap at the surface where they are caught near the cork line. In bright weather it was found advantageous to camouflage the nets, with the result that they are now all dyed green.

The records of one cannery for 1943–46 were examined to check the effect of weather on fishing. These records gave the average number of fish per boat per day and type of weather on the fishing grounds. It was noted that in general the best fishing was on bright days and that a continued period of rainy weather resulted in low catches. One week of bad weather at the peak of the season in 1945 was particularly striking in this regard. When the catch data are split into high, medium and low catches, and the weather records into rainy, dull and bright days it is evident that the bright and dull days yield about equal catches, which are higher than those of rainy days. This difference was statistically significant by the chi-square test and could be expected to occur only three times in 100 by chance alone. However, whether rainy days affect the movements of the fish or the effort of the fishermen is still an open question. That weather is only one of the factors affecting the catch is demonstrated by a comparison of the catches in 1943 and 1946. The 1946 season had about twice the rainfall of 1943, yet produced almost twice the catch.

INDEX OF EFFORT

In general, during the salmon migration every opportunity is taken to catch as many fish as possible while the season lasts and the fishing effort tends to fluctuate with the abundance of the population. The success of the sockeye catch largely determines the fishing effort directed toward the other species. For example, during the large sockeye run in 1945 the boats fished the Skeena River relentlessly; despite a strike of a week's duration at the start of the season, about 40 per cent more boat-days were fished than in 1947 when the run was small. In the latter year many boats moved off to fish other areas such as the Nass River and Rivers Inlet. In 1945 there was also a large run of pinks, but the effort directed to catch them was proportionately less than in 1947 when both the sockeye and pink salmon runs were small. Over longer periods such economic factors as the depression of the 1930's and the boom of two world wars have affected the fishing effort. Thus, it is impossible to obtain, on the basis of the data available, a true index for effort over the years. Such an index would have

to consider, among other factors, the number of boat-days of fishing, the changes in efficiency of gear and fishermen, and the changes in the fishing areas for each year. The total number of licences is the only information available which has some comparative value. In Table III adjusted totals are presented to indicate the changes due to differences in efficiency of gear and fishermen.

TRENDS IN TOTAL CATCH

Methods of Collecting and Validity of the Catch Data

The Federal Department of Fisheries has obtained catch statistics by various means. Prior to 1938 the Fisheries inspectors collected all the data. Since then each cannery has reported the catch to the Prince Rupert Fisheries office on both monthly and annual forms. All weekly pack figures were sent to the Chief Supervisor of Fisheries in Vancouver and the records of the combined Nass and Skeena pack appeared weekly in the British Columbia Canned Salmon Pack Bulletin. The monthly statistical report, showing a break-down of the catch from the Skeena River of both canned salmon and that marketed fresh, frozen or mild-cured, was the only form which gave complete data on the Skeena catch. Starting in 1947 this form was virtually abandoned and replaced by one from the Bureau of Statistics which records the total pack and by-products in hundredweights for each firm but in which the catch for the Skeena area is not separated out. The annual schedule, which was forwarded directly to the Vancouver office, was the basis for the Skeena catch figures published by the Federal Fisheries Department in their annual report. Unfortunately these forms do not cover the salmon which are handled fresh. The Provincial Fisheries Department also publishes an annual return of the salmon canned from each area. The multiple-sales slip method recommended by Dr. G. L. Burton (1949) was instituted on the Skeena River in 1950, so at the present time the total number of salmon of each species caught in each area is available regardless of how and where they are later processed.

The problem of allocating the salmon to the area in which they are caught rather than to the one where they are processed is a complicated one. Prior to 1924 the few salmon caught outside the Skeena area were not separated from the total Skeena pack. The Skeena-caught fish have always been packed on the Skeena, but since 1924 many fish have been brought in from other areas and packed in the Skeena River area. Thus the number of cases recorded as *packed* in this area prior to 1924 is considered to be more comparable to the number of cases of salmon recorded as *caught* since that date.

For sockeye salmon, care is taken to separate the catch from the pack as accurately as possible. For the other species of salmon, less care is taken and usually an approximate breakdown suffices. It is difficult to separate Skeena fish from those taken in the Nass River fishery. Fish tagged in each area have later been caught in the other. In the 1944–48 tagging experiments, only one per cent of the sockeye salmon tagged off the Skeena mouth were returned from the Nass area, but from 10 to 20 per cent of those tagged at Steamer Passage in the Nass area were taken at the mouth of the Skeena River.

Up to the early 1930's the Nass salmon catch was packed at four canneries on the river itself. With the gradual closing of these canneries from 1936 to 1945 an increased number of Nass fish have been canned on the Skeena, making it more difficult to keep the Nass and Skeena River catches separate. Many fishermen consider that sockeye salmon which are caught around Finlayson Island are bound for the Skeena River and the small amount of tagging in this area appears to bear this out, but there is no general agreement among the canneries on dividing of these fish between Nass and Skeena catches. Prior to 1935 when an eight-mile closed area from Point Ryan to Finlayson Island existed between the Nass and Skeena fishing areas, the catches could be kept separate. In recent years, fish allotted to the Nass catch are those caught in Portland Inlet or in the mouth of the Nass River itself. The Nass River catch of sockeye salmon is about one-third the size of the Skeena catch.

Age determinations of sockeye salmon recorded since 1912 (Clemens, 1950) indicate that the Nass and Skeena River catches differ in age composition. The Skeena fish are predominately of the two age-groups 4_2 (48 per cent) and 5_2 (40 per cent) whereas 65 per cent of the Nass fish are 5_3's. The Nass fish, besides differing in age, are also larger than Skeena fish. For example, the 5_3 fish from the Nass average two inches longer and one pound heavier than 5_3 fish from the Skeena. Although the fluctuations in the catches of the two river systems appear to have many features in common, marked exceptions occurred in 1940 and 1945 when the Skeena catches were high and the Nass catches were low. In 1940 the large Skeena catch was due to a large 4_2 age-class and in 1945 to a large 5_2 age-class while the failure in these years of the Nass catches was due to the small numbers in the dominant age-group, the 5_3's.

The catch figures published in the Annual Reports of the Federal Department of Fisheries will be used to evaluate the trend in the fishery, but it must be noted that they include canned salmon only, and even here there are uncertainties as to the true catch. The following two examples will suffice to indicate the difficulties involved.

(1) The sockeye catches published in the annual reports of the Federal and Provincial Fisheries Departments differ in certain years, particularly prior to 1933. In more recent years the low catch in 1942 is reported as 29,976 cases by the Federal Department and 34,544 cases by the Provincial Department. The reason appears to be in the distinction drawn between the Skeena catch and pack.

(2) A comparison of the total cases from the monthly records of the canneries and the annual Skeena catch figures for each species in 1946 follows:

	Sockeye	*Pink*	*Coho*	*Chum*	*Spring (red)*	*Spring (white)*
Monthly totals	52,650	10,614	16,093	18,859	1,122	462
Annual	52,928	10,737	26,281	11,161	2,029	410

The sockeye and pink salmon, which are largely canned, show smaller discrepancies than the other species. Many of the errors arise from the fact that the fish are transferred so often that the bookkeepers who compile the returns cannot always determine the area of capture from the cannery records.

Although a check was made on the accuracy of the catch figures during 1946–48, no successful attempt was made to collect entirely accurate figures for any one year. For our purpose, however, absolute accuracy is not required, and for sockeye and pinks at least the data give a useful picture of the relative Skeena catch from year to year.

FLUCTUATIONS IN THE CATCH FIGURES FOR EACH SPECIES, 1904–48.

The number of cases of each species of salmon *packed* on the Skeena from 1904 to 1948, and the number of cases *caught* from 1925 to 1948 as published in the annual reports of the Federal Department of Fisheries, are presented in Table IV. It should be recalled that the catch of the salmon populations spawning

TABLE IV. The pack and catch of canned salmon (in number of cases) for the Skeena river, 1904–1948, as published in the Annual Reports of the Federal Department of Fisheries. (C: *catch*—Pack of fish caught at Skeena regardless of where canned. P: *pack*—Pack at Skeena regardless of where caught.)

Year		Sockeye	Pink	Coho	Chum	Spring (white)	Spring (red)	Spring (pink & jack)
1904		93,404	30,529?	10,315	...	...	20,261	...
1905		84,717	7,523?	7,247	...	...	14,598	...
1906		86,394	...	16,867	...	...	20,138	...
1907		108,413	...	15,247	...	...	10,378	...
1908		139,846	...	10,075	...	...	13,374	...
1909		87,901	...	11,249	...	742	11,727	...
1910		187,246	13,423	11,531	...	239	9,546	...
1911		131,066	81,956	23,376	70	2,428	15,514	...
1912		92,498	97,588	39,835	504	4,501	19,322	...
1913		52,927	66,045	18,647	...	3,186	23,215	...
1914		130,166	71,021	16,378	8,329	211	11,529	...
1915		116,553	107,578	32,190	5,769	204	15,069	...
1916		60,923	73,029	47,409	17,721	2,561	18,272	...
1917		65,760	148,319	38,456	21,516	2,699	13,586	...
1918		123,322	161,727	38,759	22,573	6,828	16,013	...
1919		184,945	117,303	36,559	31,457	2,656	19,651	3,624
1920		90,869	177,679	18,068	3,834	3,123	37,403	2,198
1921		40,018	124,457	45,033	1,993	445	18,599	2,722
1922		100,615	203,555	24,673	17,668	1,805	7,080	5,591
1923		131,731	145,973	31,967	16,527	499	8,863	2,885
1924		144,732	181,338	26,907	25,603	1,301	9,511	1,361
1925	C	77,785	127,226	38,029	10,687	2,457	17,811	1,657
	P	81,149	130,083	39,168	74,308	2,603	19,185	1,657
1926	C	82,307	170,586	30,153	46,382	1,750	17,896	966
	P	82,337	210,064	30,209	63,527	1,750	17,896	966
1927	C	83,988	38,903	25,209	9,656	1,609	13,595	1,609
	P	83,984	38,761	25,623	18,659	1,609	14,856	3,567
1928	C	34,524	191,812	18,751	11,792	397	4,121	988
	P	34,559	209,579	30,194	17,751	354	5,043	988
1929	C	77,714	94,846	37,138	3,625	383	3,795	441
	P	78,014	95,305	37,456	4,835	383	3,795	441

TABLE IV (*cont'd.*)

Year		Sockeye	Pink	Coho	Chum	Spring (white)	Spring (red)	Spring (pink & jack)
1930	C	130,952	214,266	24,191	3,327	322	6,589	1,047
	P	132,372	275,642	29,203	5,057	324	6,674	1,047
1931	C	93,029	44,807	10,737	3,610	534	7,040	2,284
	P	107,936	41,264	20,146	3,893	534	7,040	2,284
1932	C	52,624	32,519	20,549	28,756	2,472	14,268	9,419
	P	59,916	58,261	48,312	38,549	2,472	16,378	9,419
1933	C	27,693	79,932	21,366	10,970	828	6,805	444
	P	30,506	95,783	39,896	15,714	227	2,626	444
1934	C	54,558	27,628	21,298	6,242	860	6,809	592
	P	70,654	125,163	54,470	24,388	860	6,844	492
1935	C	52,879	81,868	8,122	23,498	188	3,422	429
	P	64,140	99,412	45,512	31,807	188	3,443	429
1936	C	81,960	92,997	32,142	15,343	356	3,781	414
	P	97,823	178,299	55,198	36,892	435	4,883	455
1937	C	41,023	57,623	14,573	10,027	315	3,704	382
	P	55,811	72,455	34,502	37,431	315	3,788	382
1938	C	46,988	69,299	38,542	14,668	259	2,916	1,141
	P	73,580	146,676	100,658	34,785	259	3,361	1,165
1939	C	68,388	91,559	27,115	6,360	336	3,124	1,396
	P	96,358	127,521	48,973	15,666	348	3,277	1,488
1940	C	116,505	46,687	19,196	4,684	396	4,708	1,017
	P	133,854	91,612	62,516	62,114	571	5,884	1,113
1941	C	81,183	51,389	45,891	12,138	368	3,929	641
	P	110,544	73,896	126,557	54,357	448	4,695	703
1942	C	29,976	47,819	36,396	10,611	617	5,305	699
	P	57,539	146,322	70,385	31,481	832	5,850	874
1943	C	28,259	53,203	40,281	6,408	379	964	441
	P	51,476	122,040	63,639	57,580	623	1,443	839
1944	C	67,855	45,833	18,810	7,173	193	899	468
	P	92,203	190,872	38,160	87,072	289	1,176	664
1945	C	103,940	69,149	33,673	9,121	363	1,208	785
	P	117,860	211,140	51,905	44,104	389	1,324	827
1946	C	52,928	10,737	26,282	11,161	410	1,591	438
	P	72,319	50,799	38,534	81,633	551	1,864	579
1947	C	32,511	13,184	12,766	8,224	414	1,376	326
	P	65,429	47,831	35,522	87,476	531	1,688	398
1948	C	101,268	50,656	16,133	11,863	593	3,133	99
	P	121,699	153,213	41,146	108,622	764	3,824	143

in the Skeena is probably best represented by the *pack* figures up to 1924 and the *catch* figures after that date.

SOCKEYE SALMON

Since most sockeye are eventually canned the number of cases given in Table IV and Figure 4 represents the relative catch from year to year. In such a competitive fishery, where probably half of a limited population is caught within

a short period during the spawning run, the effort is markedly regulated by the size of the catch, both within and between seasons. Moreover, since a precise index of effort is not available, the commercial catch alone provides the most adequate index of relative population size. No doubt the magnitude of the fluctuations in the catch is less than in the total population but since accurate estimates of the escapements are not available the absolute sizes of the populations are unknown.

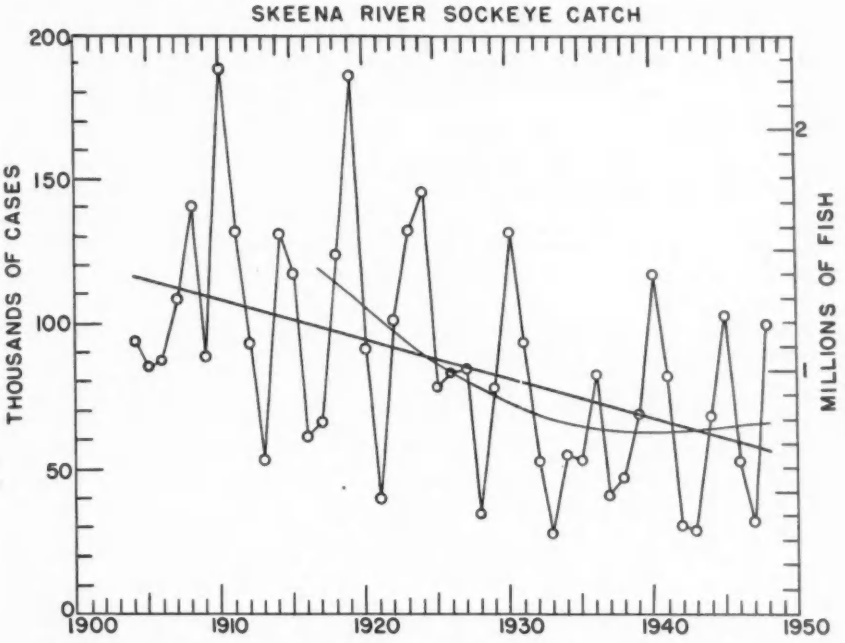

FIGURE 4. The catch of sockeye salmon from the Skeena River area, 1904–48. The heavy trend lines were fitted by a straight line (1904–48) and by a second degree polynomial, 1917–48.

Prior to the turn of the century the catches increased with the development of the fishery, until in 1910 a peak of over 185,000 cases was reached. The over-all trend line indicates a general decline of about 50 per cent or an average decrease of 1,300 cases per annum. The shorter trend line, computed since 1917 when detailed age determinations were started, indicates a period of gradual decline in the catches prior to about 1935 and a period of levelling off since then. It should be noted that it was during this period of decline that the number of Japanese licences decreased (1923–26) and the river boundaries were lowered (1925 and 1935). The concurrent trends in effort will be discussed in a later section.

Although the fluctuations of the Skeena sockeye catch are large and irregular, varying as much as fourfold from one year to another, with peaks from two to six years apart, it is apparent that there has been a marked decline since 1910, with a tendency to level off in recent years.

PINK SALMON

Over 90 per cent of the pink salmon in this area are canned; the few which are handled fresh are used either as fillets or bait. The effort devoted to the catch of Skeena pinks varies from year to year in that it is affected by the size of the sockeye catch made earlier in the same year. Because the majority of the pink salmon packed on the Skeena in recent years have been brought in from other areas, the figures for pink salmon caught on the Skeena are much less reliable than those for sockeye.

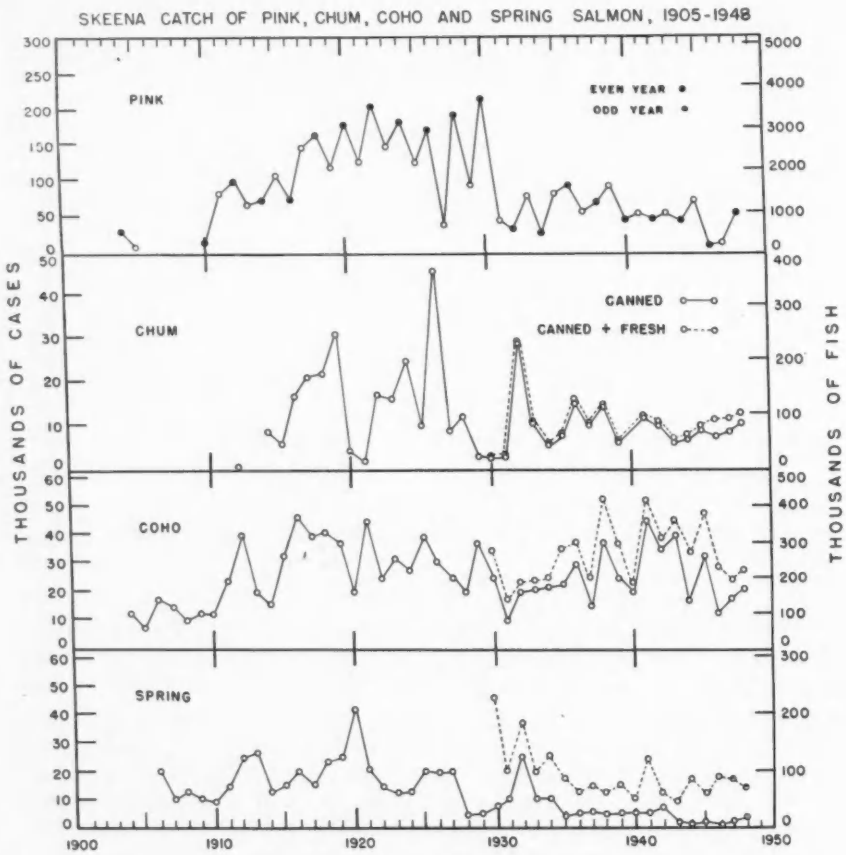

FIGURE 5. The catch of pink, chum, coho and spring salmon from the Skeena River area, indicating the proportion used by the fresh fish and canning industries.

With these reservations, the catch figures for Skeena pink salmon, presented in Table IV, are shown in Figure 5 in order to portray the general trend for this species. The pink salmon fishery commenced prior to 1910 and reached a peak catch from 1920 to 1930, during which period the even year population was the larger one. Since these fish all mature at two years of age, two separate populations are present in the odd and even years. The large even-year run of 1930 failed to repeat itself in 1932. The same thing happened in that year to catches from other northern British Columbia districts, and probably the cause was the same in all cases. Since 1930 the catch of this cycle has been greatly reduced, with the catch in the even years often smaller than that in the odd years. The catches made in 1946 and 1947 were record lows for both cycles.

CHUM, COHO AND SPRING SALMON

A large proportion of chum, coho and spring salmon is handled fresh, so it was necessary to determine these quantities and add them to the quantity canned. Data on fresh fish were supplied by the Prince Rupert office of the Federal Department of Fisheries. Care was taken to separate the Skeena catch from the Skeena pack as effectively as possible. To convert number of cases and hundredweights of salmon into numbers of fish, the values in Table V were used.

TABLE V. Average weight per fish and number of fish per case for Skeena river salmon. (Approximately 72 pounds of raw fish are required to make a 48-pound case of canned salmon.)

Species	Pounds per fish	Fish per case
Sockeye	6	12
Pink	4	18
Chum	9	8
Coho	9	8
Red spring	12	6
White spring	18	4
Jack spring	4	18

The best estimates of the number of Skeena-caught fish which are handled fresh are presented in Table VI. The total catches of chum, coho and spring salmon are shown in Figure 5, based on Table IV (the number of cases canned) and Table VI (the numbers of fish handled fresh).

Most of the *chum salmon* are canned. The chum salmon catch fluctuated greatly from the start of the fishery, about 1915, down to the year 1932. Since 1932 it has remained more uniform, but it has never been as important as that of any of the other species.

Since 1904 the *coho salmon* catch has increased steadily, with the largest catches recorded in 1938 and 1941. In recent years the fresh-fish houses have handled more of the fish, between 25 and 60 per cent of the catch. Because they are captured by trolling far out in the ocean, it is impossible to obtain a true picture of the Skeena coho population from the Skeena catch figures alone.

As in the case of coho salmon, it is difficult to obtain a true picture of the Skeena population of *spring salmon*, for in recent years the fresh-fish industry has

TABLE VI. Skeena catch handled fresh, 1930–1948, in thousands of fish. (The method of estimation was different for the years 1930–1940 and 1941–1948.)

Year	Sockeye	Pink	Coho	Chum	Spring
1930	...	...	87	5	150
1931	...	...	60	15	36
1932	...	12	22	15	34
1933	...	...	22	10	38
1934	...	12	22	5	64
1935	...	25	100	15	48
1936	...	...	55	...	23
1937	...	12	105	10	30
1938	...	25	120	5	30
1939	...	50	105	5	40
1940	...	35	28	5	16
1941	1	35	54	...	96
1942	...	37	23	2	23
1943	1	20	45	2	38
1944	3	68	134	7	76
1945	2	118	105	8	49
1946	4	21	106	26	78
1947	1	7	67	22	70
1948	...	70	92	13	57

handled from 60 to 90 per cent of the fish. The exceptional number handled fresh in 1930 was probably composed of a large number of spring salmon from rivers other than the Skeena. The percentage mild-cured varies from 1 to 25, while that canned varies from 5 to 30. From 5 to 30 per cent of the spring salmon caught have white flesh and are marketed at a reduced price.

DETAILED TRENDS IN THE CATCH AND EFFORT FOR SOCKEYE SALMON, 1935–48

Lacking detailed data for the total Skeena sockeye catch and effort, data were used from a group of fishermen for which daily records were available back to 1935. The catch and effort data of this sample (Fig. 6) when compared to that of the whole fishery (Fig. 3, 4) indicate that the sample, which comprises about one quarter of the total fishery, is fairly representative of the fishery.

In considering the data summarized in Figure 6 it should be noted that, up to 1941, about 50 per cent of the fishermen were Japanese. The Japanese fished a longer season (2 to 4 days more than the Indians and 2 to 9 days more than the Whites); they also must have fished longer hours or more effectively each day, since the average daily catch from 1935 to 1941 (Fig. 6C) is 37 for the Japanese and 29 for both the White and Indian fishermen. During this same period the Japanese caught an average of 1,378 sockeye per season, the Indians 1,023 and the Whites 922. Since the withdrawal of the Japanese in 1941 the intensity of the fishing effort (Fig. 6B) and the number of fish caught (Fig. 6A) have been lower. If the Japanese had continued fishing, the total catch and effort after 1941 would no doubt have been higher. The fact that the Indians and

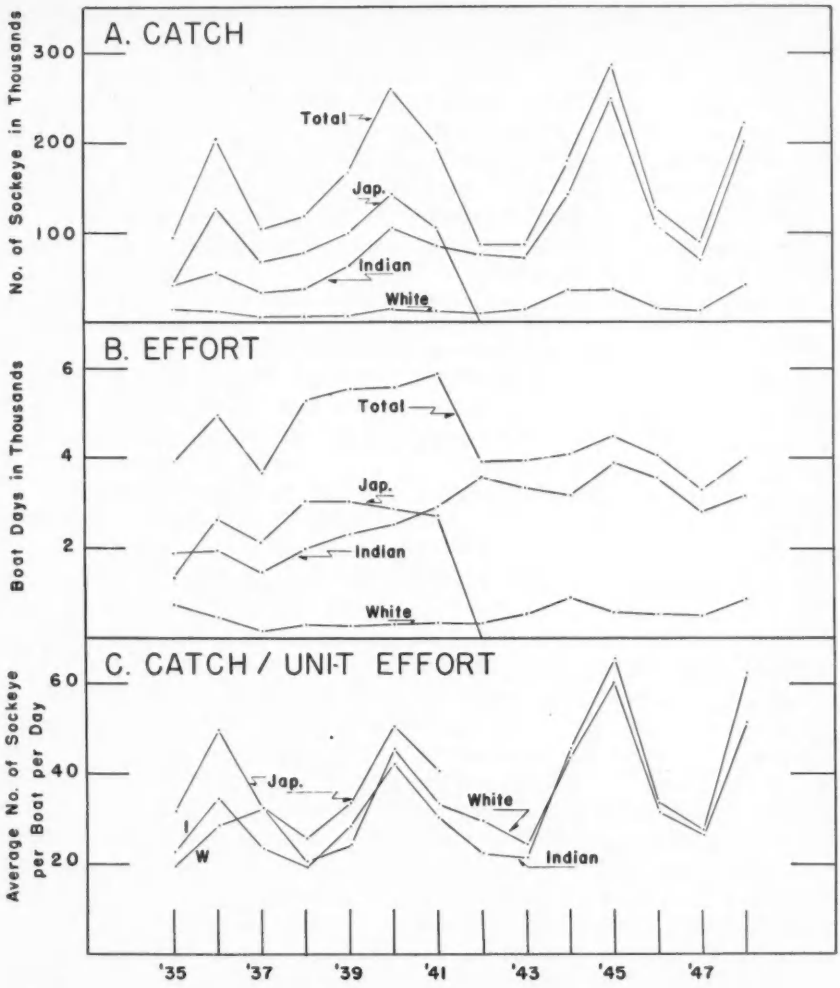

FIGURE 6. Catch (A), effort (B) and catch per unit effort (C) for a sample of the fishermen in the sockeye salmon fishery.

Whites only partially replaced the fishing effort of the Japanese after 1941 must account in part for the extremely low catches in 1942 and 1943.

Only power boats are involved in the sample. The net-drum, which was introduced in 1942 after the Japanese left, was in general use by 1944. When all factors which might affect the fishing are considered, it appears that the catches and catches per unit effort for the period were at least maintaining themselves with peaks four, five and three years apart. The catch in 1945 would have been

larger if there had not been a strike at the beginning of the season. Therefore we might infer from the sample data that the sockeye population, although fluctuating widely, has not been trending downward during the last 14 years.

The weekly number of fish caught by the sample group is shown cumulatively in Figure 7. These data indicate that the run is under way when the fishing season starts but is virtually over when the fishing season is closed around the middle of August. Prior to July 10 the fishing fleet is not at full strength and after August 10 the effort falls off rapidly. Over the years the heavier exploitation during the latter half of the season may have had some effect on the relative size of the runs to the various tributaries.

There is considerable variation in the catch from week to week (Fig. 7).

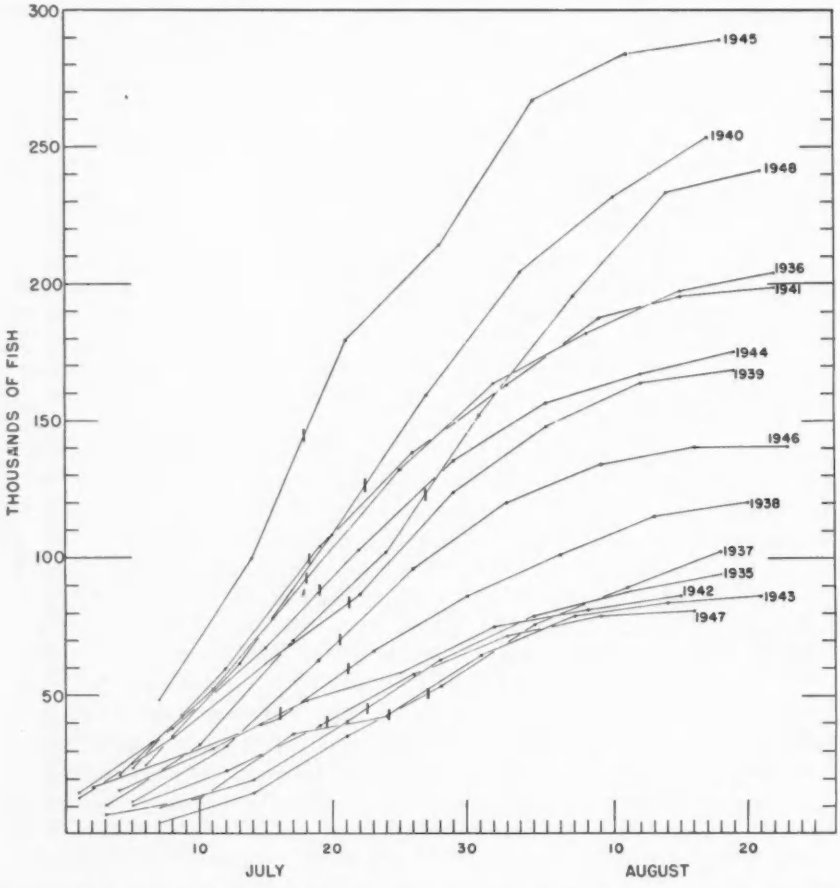

FIGURE 7. Seasonal occurrence of the Skeena sockeye run, 1935 to 1948, based on the cumulative weekly catches from a sample group. Vertical lines mark 50 percentile points.

This is sometimes due to weather conditions adversely affecting the fishing and at other times due to fluctuations in the size of the run. Thus, analysis of the first few weeks of fishing provides only a general prediction of the ultimate size of the run in progress. The catch during 1948 was most aberrant in this respect. The time at which 50 per cent of the catch in each year was taken (Fig. 7) has varied from July 16 to July 27. The exceptionally large catches toward the end of the season in 1948 were associated in part with the abnormal weather conditions, which caused great floods and hence poor fishing in the early part of the season, and in part to the occurrence of a large proportion of 4_2 fish, which tend to come later than the 5_2's.

General Trends in the Catch and Effort for Sockeye Salmon, 1904–48

The number of gill-net licences issued each year have been presented in Table III and Figure 3. It has been noted previously that these data do not represent the true fishing effort each year, but for the following discussion they should adequately represent the general trends in the effort.

The sockeye catch figures, Table IV and Figure 4, represent the commercial exploitation with reasonable accuracy. In general the size of the catch tends to regulate the intensity of the effort both within and between seasons, because it is economically unsound to continue operations unless a profitable catch per unit of effort is achieved. Thus, within limits, a balance between the catch and effort is maintained.

To consider the general history of the fishery, when fishery started in 1877 there existed a large population of sockeye salmon in a natural state. The rate of mortality through physical and biological causes would be in balance with the rate of increase through reproduction. With the fishery acting as a predator, the size of the population would drop, the survival rates would increase to counteract this new drain and the size of the population would tend to reach a balance at new levels. Prior to 1900 the total catch increased with the increase in fishing effort. Following this early period of exploitation and underfishing for which detailed records are not available, the catch reached a peak around 1910 and started to decrease gradually. The effort continued to increase until the period 1925–30 when it was maintained at an average level of over 1,100 gill-net boats. Much of this fleet operated in the river above the present fishing boundaries. During this period of high effort the total catch dropped off at a faster rate than formerly. If overfishing is defined as the condition of a fishery in which the more you fish the less you catch, then it was during this period that overfishing was occurring. Since about 1935 the effort has gradually decreased for economic reasons and as a result of restrictive regulations, and the catch has tended to level off. Recent catches from 1948 to 1952 suggest the commencement of a period of increase in catch. However, when the catches obtained by 800 gasoline boats in recent years are compared to the catches of twice the size made around 1910 by 800 sail boats, it is clear that a great change has taken place in the size of the sockeye population. It is difficult to determine the number of fishing units by which the maximum steady yield would be maintained, but it is at some intermediate level between these two periods.

In Figure 8 the data of catch and effort have been smoothed by a moving average of five years to indicate these general trends. The catch appears to fluctuate more than the effort. At present the keen competition in fishing a limited population with efficient gear is being restricted by law and for economic reasons. If the adverse factors which have been or are affecting the natural survival are alleviated as much as possible, the size of the population should increase somewhat from its present level.

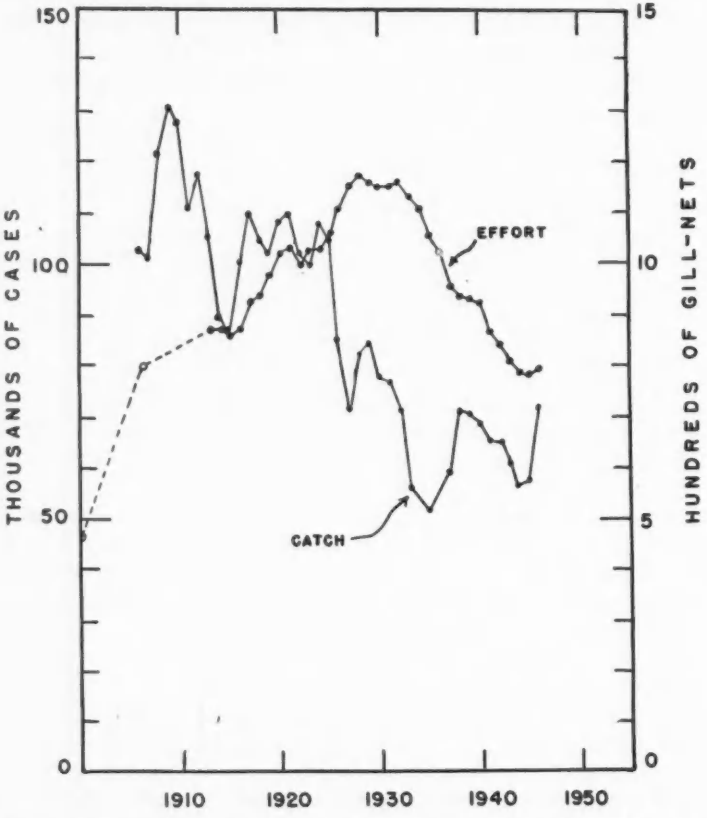

FIGURE 8. The catch and effort in the Skeena River sockeye salmon fishery based on data in Tables III and IV smoothed by a moving average of 5 years.

CYCLES IN THE CATCH AS A POSSIBLE BASIS FOR PREDICTION

SOCKEYE SALMON

The Skeena River sockeye catch (Fig. 4) has been shown to fluctuate about a gradually decreasing trend line with peaks 2 to 6 years apart. For successful prediction an understanding of these short-term cycles in the catch is essential.

The fluctuations are the result of many factors which affect the size and age composition of the spawning escapement and the subsequent survival of the young salmon in both the fresh and salt water stages. Precise data on these topics are not available. Fortunately the age composition of the sockeye catch has been obtained since 1912 (Clemens, 1950), and a study of the age-classes may throw some light on the fluctuations in the catch.

TABLE VII. The percentage of each age-group and the total number of cases (in thousands) of sockeye salmon caught in the Skeena River from 1917 to 1948.

Year	% 4_2	% 5_2	% 5_3	% 6_3	Total catch	Total catch index[a]	Predicted catch index[b]
1917	57	29	9	5	66	55	...
18	51	34	9	6	123	107	...
19	27	60	9	4	185	167	...
20	15	71	6	8	91	85	...
21	69	22	6	3	40	39	...
22	70	16	12	2	101	103	...
23	56	29	8	7	132	138	94
24	23	69	7	1	145	159	134
25	51	45	3	1	78	89	99
26	62	26	9	3	82	96	90
27	62	28	9	1	84	102	106
28	51	39	7	3	35	44	90
29	62	30	6	2	78	101	176
30	39	52	8	1	131	177	105
31	40	30	28	2	93	129	98
32	44	37	7	12	53	76	63
33	57	36	5	2	28	41	84
34	58	34	7	1	55	82	106
35	49	31	18	2	53	80	159
36	67	20	11	2	82	126	110
37	45	40	11	4	41	64	59
38	64	15	16	5	47	75	74
39	50	35	11	4	68	108	74
40	80	15	4	1	117	186	124
41	39	52	8	1	81	129	70
42	36	54	7	3	30	48	83
43	39	39	16	6	28	44	80
44	37	52	7	4	68	106	203
45	20	63	12	5	104	160	89
46	13	70	8	9	53	80	96
47	14	82	3	1	33	49	47
48	80	13	6	1	101	149	64
Av.	47.7	39.6	9.2	3.5			

[a]Indices were calculated as the ratio of each year's catch to the average catch determined from the curved trend line (Fig. 4) which was considered to equal 100.

[b]This index is the total of the individual catch indices for each age-class caught in the respective parent years.

The age data are based on random scale samples taken from two to three thousand fish in the commercial catch each year. The collections were made throughout the entire fishing season from the commercial sockeye catch at one of the larger canneries. For the first few seasons only two age-classes are recorded. On the basis that the sampling adequately represents the four age-classes in the Skeena River catch since 1917, the percentage of each age-class and the total number of cases of sockeye caught are shown in Table VII. The majority of the fish are 4 and 5 years of age, these being approximately equal in numbers when averaged over the whole period, but exhibiting large annual variations.

HEREDITARY AND ENVIRONMENTAL INFLUENCES UPON AGE AT MATURITY

An attempt was made to decide whether age at maturity is determined more by hereditary or by environmental influences, for the two major age-classes. To eliminate the trend in the catches a curved line (Fig. 4) was fitted by means of the equation $\hat{y} = 120.3 - 4.87x^2$, where $\hat{y}$ is the estimated "average" catch and x is the year ($1917 = 0$). The trend line was considered equal to 100 and the ratio calculated for each year's catch was expressed as a percentage of the calculated "average" for that year (Table VII). This index was then divided in proportion to the ages in the sample, giving indices for each age-class separately. In order that large fluctuations should not contribute unduly to the correlation values, the data were transposed to logarithms. The correlations obtained are shown in Table VIII.

TABLE VIII. Correlations (r) between parental and progeny age-class indices for Skeena River sockeye salmon from 1917 to 1948. An asterisk indicates a statistically significant relationship.

	Parents	Offspring	Number of years	r	P
A	4_2 in year n	4_2 in year $n+4$	28	0.44	$<.05$*
B	5_2 in year n	5_2 in year $n+5$	27	0.49	$<.01$*
C	5_2 in year n	4_2 in year $n+4$	28	0.21	$>.05$
D	4_2 in year n	5_2 in year $n+5$	27	0.39	$<.05$*
E	4_2 plus 5_2 plus 5_3 plus 6_2 in year n	4_2 in year $n+4$, plus 5_2 in year $n+5$, plus 5_3 in year $n+5$, plus 6_2 in year $n+6$	26	0.44	$<.05$*
F	4_2 year in $n-4$, plus 5_2 in year $n-5$, plus 5_3 in year $n-5$, plus 6_3 in year $n-6$	4_2 plus 5_2 plus 5_3 plus 6_2 in year n	26	0.35	$>.05$
G[a]	4_2 in year n	5_2 in year $n+1$	31	0.41	$<.05$*

[a]Here the correlation is between members of the same brood, rather than between parents and offspring.

If there were no *hereditary* influence in the determination of age at maturity, then the correlation values for A and C should be equal (apart from sampling variation), as should B and D. Actually A is greater than C and B is greater than D; and the combined probabilities of significance of the differences between the two pairs is about 80 per cent ($P = 0.2$). Hence there is some indication of an hereditary influence upon age at maturity, but it cannot be established from these data.

If there were no *environmental* influence in the determination of age at maturity, the correlation values for A and B should be positive and those for C and D should be zero. Actually the C and D correlations are both positive; the combined estimate is 0.30, which differs from zero with 90 per cent probability ($P = 0.1$). Hence there is some indication of environmental influence upon age at maturity, but it too cannot be proven.

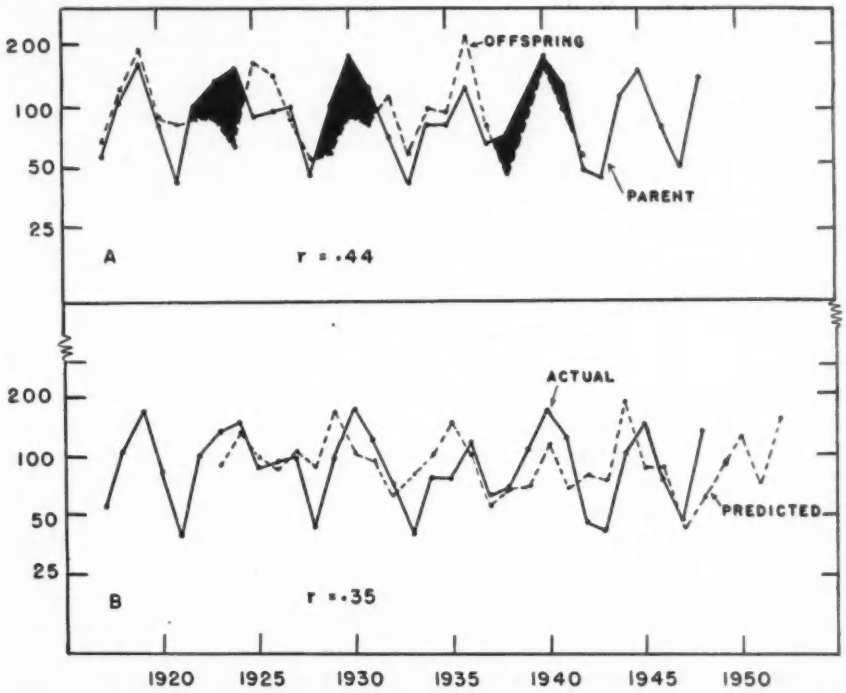

FIGURE 9. Reproduction indices for sockeye salmon, in terms of the "normal" catch indicated by the curved trend line of Figure 4. (A) "RETURN" INDEX: The catch in each parental year (as percentage of the "normal"–solid line) is compared with the sum of the observed progeny catches (as percentages of the "normal" for their respective years–dotted line). (B) PREDICTION INDEX: The actual catch in each year (as percentage of "normal"–solid line), is compared with a predicted catch (dotted line) obtained by summing the percentage contributions of the fish of appropriate ages in respective parental years. The catch indices (Table VII) are plotted on a logarithmic scale.

It can be argued that age at maturity could scarcely be determined by chance: it must be the result of either hereditary or environmental factors, or both. Hence the above P-values, which are of the same order of size for the two effects, may constitute evidence that both effects are in operation. The failure to obtain a more clear-cut picture springs from the inadequacies of the data. One source of variability is that, even if the samples used for age determination always adequately represent the catch (which is far from certain), they are not likely to be as good a representation of age composition of the spawning escapement, because of the selective action of the gill-net fishery. Also, variations in natural survival rate of the salmon, both in fresh and in salt water, result in a variable relationship between spawning escapement and ocean return. Finally, the ratio of catch to stock may vary between years, and also within a year.

PREDICTION OF CATCHES FROM INDICES OF PARENTAL YEARS

To obtain an over-all relationship between catches of parental and progeny years there are two possible procedures. First, the index of total catch for year n may be related to the sum of the indices for appropriate ages four, five and six years later. This correlation, shown in line E of Table VIII, is equal to 0.44, suggesting that only 19 per cent of the variation in the offspring catch is associated with variation in the parent catch. These data are presented in Figure 9A, and indicate three periods of failure of the offspring catches to maintain the parent catch of each brood year. This graph is similar to the "index to the success of return" used by Thompson (1945) in a percentage form. The periods of failure around 1923 and 1930 were most critical in producing the over-all decline in the sockeye catch shown in Figure 4.

The relationship just discussed cannot be used to predict catches in advance, because it becomes available only after all of the progeny generations have been taken. For purposes of prediction it is necessary to estimate the catch in year n from the catches of appropriately aged fish in years $n - 4$, $n - 5$ and $n - 6$ (Table VIII, line F). This correlation is only 0.35, which suggests that only 12 per cent of the offspring variation is dependent on the variation in parent catch. The data for this "index of prediction" are presented in Table VII and in Figure 9B to show that catches predicted on this basis have limited practical usefulness, since they may vary from one-half to twice the size of the actual catch index.

Both the E and the F correlations above presuppose an hereditary effect in determination of age at maturity, but they differ in respect to where environmental effects producing differences in survival are most active. With E, all the parents spawn in the same brood year and all the young are reared for a year under the same freshwater conditions but mature in different years in the ocean. With F, the parents spawn in different brood years; the young are reared under different freshwater influences, but they mature in the same year and all have had the same two final years of life in the ocean. Though the difference between the correlations 0.44 and 0.35 is not significant, the higher value for the E series may suggest a greater importance of the freshwater phase in determining over-all survival.

Recent catches indicate a high survival from the 1944 brood year. It was previously mentioned that in 1947 the sockeye escapement included a large number of three-year-old males. This was followed by a large number of 4_2 fish (80 per cent or 81,000 cases) in the catch of 1948, and of 5_2 fish (76 per cent or 50,000 cases) in 1949. Over past years the relationship between 4_2 fish in the catch and 5_2 fish in the catch the following year (G, Table VIII) is significant ($r = 0.41$), but the variation is sufficiently great to prevent useful predictions being made on this basis. However it does further substantiate the importance of the freshwater environmental influences on the survival of the young.

In summary, commercial catch data suggest influences of both hereditary and environment on age at maturity and rate of survival, but the relationships are not precise enough to provide a basis for useful prediction of the size of the sockeye population which will be available to the fishery. Before a reliable basis can be established, detailed information on the spawning escapement and subsequent survival of the offspring in both fresh and salt water must be obtained for a series of years. Such information is currently being accumulated.

Pink Salmon

Pink salmon invariably mature at two years of age. Thus the odd- and even-year catches are from two distinct populations and the offspring catch is associated solely with the parent catch two years earlier. The offspring and parent catches are shown in Figure 10, A and B, for both odd- and even-year cycles. In the odd-year population the drastic failures of the brood years 1925, 1929 and 1945, and in the even-year population the failure of the brood years 1930 and 1944, have had a marked effect on the trend in the catches. If predictions are based on a two-year cycle in the catches (Fig. 10C), it is apparent that they would have been useful only for the period 1919–31 and to a lesser extent for 1940–46. The numerous factors which affect the size of the catch, escapement and resulting return are apparently too variable to provide reliable predictions of the offspring catch on the basis of the catch in the parent year.

The periods of marked failure in the offspring catches cannot be attributed to abrupt changes in fishing effort and, since the escapements were apparently good, the conditions for survival must have been extremely adverse either in the streams or in the ocean. The water conditions in the streams during the years 1944 and 1945 will be discussed briefly. The rainfall data for the lower Skeena indicate that August and September of 1945 were exceptionally dry months, which corroborates the field observations that pink salmon had difficulty ascending from the main river into the tributary streams and that the areas available for spawning were reduced. Following this dry period, exceptionally heavy rainfall in October and November resulted in freshets which scoured the spawning beds thoroughly. In 1944 the conditions were reversed, as the rainfall was heavy during July, August and September and light during October, November and December. This would result in easy access to the spawning beds, but probably many eggs either dried out or were damaged by frost during the following winter. Consequently the failure of the 1946 and 1947 catches may have been due to different adverse conditions in the streams.

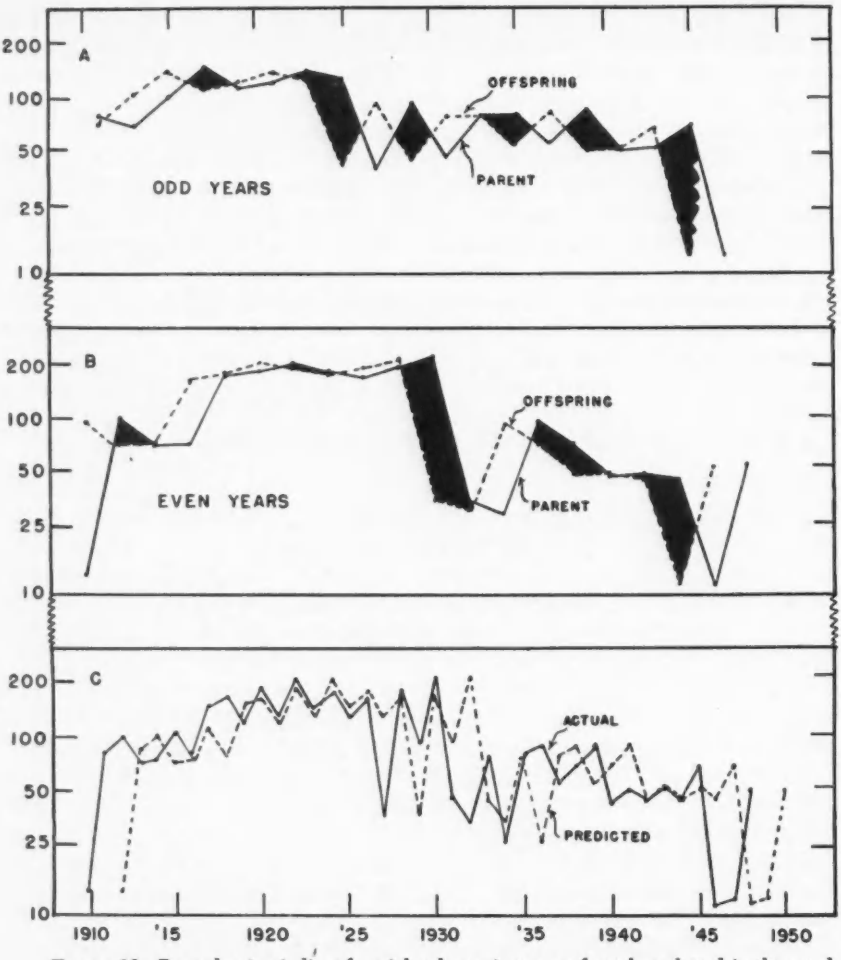

FIGURE 10. Reproduction indices for pink salmon, in terms of catches plotted in thousands of cases on a logarithmic scale. (A) "Return" index for the odd-year cycle. (B) "Return" index for the even-year cycle. (C) Prediction index.

If the Skeena River pink salmon catches were more representative of the total population and if survival records were available for the pink spawning areas for a number of years, a useful prediction of the catch should be feasible.

RELATIONSHIP OF CATCH AND ESCAPEMENT OF SOCKEYE SALMON, 1944–48

In any study of a commercial salmon fishery of the most important objectives is to determine the relationship between the catch and escapement for the watershed concerned, so that an optimum balance can be established and the

maximum safe exploitation can be obtained. The catch of the commercial fishery is probably recorded with an error of less than 10 per cent, and the much smaller catch by the Indian food fishery with an error of less than 50 per cent. Estimating the escapement to a large river system such as the Skeena River is much more difficult than determining the catch. The methods used and the results achieved for the period 1944 to 1948 have been summarized by Brett (1952), but there is still a need for improving the accuracy of present estimates. Each year the spawning grounds were closely inspected and counts were made of the fish in accordance with standard procedures. The construction and operation of a counting fence on the Babine River made possible a count of all the fish entering the most important sockeye spawning area in the system. A comparison between observer's estimates and the actual fence counts at Babine showed that the estimates were approximately one-half of the actual counts.

The returns from salmon taggings off the mouth of the Skeena River (Pritchard, 1945, 1946, 1947, 1948; Milne, 1949) provide another method for estimating the Indian catch and the spawning escapement. Each year approximately 2,000 sockeye salmon were caught in the commercial gill-net area by means of a chartered purse-seine boat, tagged with plastic discs and released. Many of these tagged fish were subsequently recovered from the gill-net fishery at the river mouth, from the Indian fishery at various locations on the river and from the spawning grounds. The high proportion of tags returned from the Indian fishery is difficult to explain. It is possible that the Indians returned a few tags upriver which were actually caught in the ocean and commercial fishery, or in certain places they may be able to fish selectively for tags. Only a few tags were recovered from the spawning grounds. The number of tags that cannot be accounted for, if used as an estimate of the escapement, after the commercial and Indian tag returns are deducted, is usually too high. It includes tags which have been lost from the fish and those recovered but not turned in, as well as those actually present on spawning fish. Thus, estimates of the escapement based on ocean tagging are high, while estimates based on observations are low.

For 1944–48 the best estimates for the escapement no doubt lie part way between these two extremes. From general observations, Indians catch only what they need for food, and tend to fish more heavily in a poor year and more lightly in a good year. Therefore the Indian catch probably remains at a more constant level than either the commercial catch or the escapement.

In Table IX estimates of the fraction of the stock taken commercially are large (50 to 75 per cent) when based on observations of the escapement but are small (19 to 41 per cent) when based on tag returns. The estimates of the Indian catch and spawning escapement are correspondingly small when based on direct observations, and are large when calculated from tag recoveries. The tagging estimates are more erratic, and are difficult to rationalize, unless it is borne in mind that the tags are not randomly distributed throughout the population but were placed on the fish during the first half of the run when the fish were part way through the fishery.

The true average situation is probably close to a spawning escapement of

TABLE IX. Estimates of Skeena sockeye population, 1944–48.

	1944		1945		1946		1947		1948	
	No. of fish	%	No. of fish	%	No. of fish	%	No. of fish	%	No. of fish	%
Observational estimates										
Commercial	807,000	70	1,227,000	71	621,000	62	385,000	50	1,200,000	75
Indian fishery	58,000	5	56,000	3	39,000	4	41,000	5	50,000	3
Escapement	285,000	25	447,000	26	341,000	34	345,000	45	350,000	22
	1,150,000	100	1,730,000	100	1,001,000	100	771,000	100	1,600,000	100
Tagging estimates										
Commercial	807,000	41	1,227,000	26	621,000	30	385,000	19	1,200,000	22
Indian fishery	138,000	7	425,000	9	207,000	10	243,000	12	600,000	11
Escapement	1,020,000	52	3,060,000	65	1,240,000	60	1,400,000	69	3,700,000	67
	1,965,000	100	4,712,000	100	2,068,000	100	2,028,000	100	5,500,000	100
Best estimates										
Commercial	807,000	53	1,227,000	45	621,000	45	385,000	34	1,200,000	48
Indian fishery	90,000	6	150,000	5	75,000	5	70,000	6	150,000	6
Escapement	620,000	41	1,360,000	50	680,000	50	690,000	60[a]	1,150,000	46
	1,517,000	100	2,737,000	100	1,376,000	100	1,145,000	100	2,500,000	100

[a]The escapement to Babine Lake in 1947 included 261,000 three-year-old males. Considering only the older fish, the 1947 escapement is only 50 per cent of the total stock. In other years the "jacks" were not numerous enough to distort the relationship appreciably.

50 per cent, a commercial catch of 45 per cent and Indian catch of 5 per cent. This approaches the requirements of the "White Act" in Alaska which provides for an escapement of 50 per cent of the population. Since the Skeena catches for recent years appears to be fluctuating in balance with the natural survival rates without producing a further decline, a catch of 50 per cent is probably approaching the optimum exploitation which the present Skeena sockeye salmon population can support.

DISCUSSION OF THE SOCKEYE SALMON FISHERY REGULATIONS

The Skeena sockeye salmon catches show a gradual decline followed by a recent levelling off. The pertinent problem is how to build up the population so the maximum surplus can be harvested without endangering future use. So many factors are involved that no single measure will probably suffice to improve the situation quickly and efficiently. During the survey from 1944 to 1948, no convincing evidence was found for any change in the freshwater environment of the sockeye salmon which would impose significant added hazards to the success of spawning in recent years, and the decline was attributed mainly to the commercial fishery (Pritchard, 1948–49). Since then, a natural rock slide has occurred which partially blocked the important Babine River in 1951 (Godfrey *et al.*, 1954). This slide has now been removed. It is possible that points of difficult passage, either here or elsewhere, have affected the salmon runs. The final solution will probably involve both changes in the fishing and implementation of proven methods to increase the natural survival rates.

A few possible changes in the fishing regulations will be discussed briefly. The effect of man's exploitation has been examined as a possible cause for the decline in the sockeye salmon population. The canners themselves fully realize that their present efficient methods, if unchecked, could almost eliminate the sockeye population. The fact that no decline has occurred in the catches in recent years would suggest that the effort may have been sufficiently restricted by regulations and by economic considerations for the present size of the population. Also there is no guarantee that a substantial restriction of present effort would be followed by a high catch, as might be anticipated, because unidentified factors of survival in the watershed or in the sea may be more important than the fishery. Nevertheless the following changes in the regulations appear warranted.

The start of the fishing season has been set each year in the latter part of June while the closing date around the middle of August has been dictated by the lack of fish to be caught. Thus over the years the later portion of the run appears to have been more heavily fished. Since this is composed largely of 4_2 females, it has been suggested that the season be terminated earlier. By opening the season earlier the older males, which precede the females, could be more heavily exploited. For the period 1936 to 1948 the annual samples of the catch have averaged 61 per cent females. Few small "jacks" are caught by the present commercial nets. The selective action of the gill-nets must also be considered in any attempt to produce a more evenly balanced sex ratio in the catch and the escapement.

The results of five years of ocean tagging, 1944–48, have shown that two-thirds of the sockeye require more than two days to move from the tagging area off the mouth of the river to the river boundary, and that a few fish spend as long as a month in this area. Hence the present 48-hour closed weekend period is only partially effective. In order to make the weekend closure more effective the period could be extended. Lowering the river boundary, or changing the ocean boundary back to Point Ryan where it was prior to 1935, would have similar effects. Such a change in the ocean limits would have the added advantage of leaving a gap between the Nass and Skeena areas. In this way a more accurate separation of the catches from the two rivers would be possible. In the past the lowering of the river boundary has been largely negated by the extension of the ocean fishery.

For any change in regulations, it is vital that the effect on catch and escapement be recorded by adequate data. Only in this way can the most effective combination of fishing regulations be used, to achieve the desired result of increasing the production of sockeye salmon in the Skeena River.

SUMMARY

The Skeena commercial salmon fishery commenced with the opening of the first cannery in 1877 and expanded greatly by exploiting a greater variety of species and stocks, until in 1948 it supported numerous modern canneries and fresh-fish establishments. The changes in fishing areas, seasons and methods of fishing, which have been described in detail for the important sockeye salmon gill-net fishery, make it difficult to determine an adequate index for effort over the years.

The methods and difficulties of obtaining catch and effort statistics for the Skeena River salmon populations in past years emphasizes the need for improving the accuracy of their collection in the future. The new multiple-sales slip system should satisfy this need.

On the basis of the catch data available for each species of salmon the probable trends in population sizes are indicated. For sockeye salmon the catch attained a maximum of 187,000 cases (about 2,250,000 fish) in 1910 and since then has declined to minima of 28,000 cases (about 335,000 fish) in 1933 and 1943. In recent years the catches have tended to level off. For pink salmon the catches declined drastically after 1930, especially in the even-year cycle. In 1946 and 1947 record lows were caught in both odd- and even-year cycles, but there was substantial recovery subsequently. The smaller chum salmon catches appear to have declined in recent years to provide a more uniform catch than in the earlier years. Owing to the difficulty of separating the spring and coho salmon catches into Skeena River fish, it is not possible to state whether or not the catches of these species have declined.

An analysis of the age-cycles in the annual catches of both sockeye and pink salmon indicates that these data alone do not provide a reliable basis for making useful predictions of future catches. Detailed information on the size of the

escapements and on the fluctuations in survival in both the freshwater and ocean environments is needed before a sound system of regulations can be established, and is now being obtained.

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